THE CONTEMPORARY SCIENCE SERIES

THE EVOLUTION OF SEX

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EVOLUTION OF SEX.

BY

PROFESSORS PATRICK GEDDES

AND

J. ARTHUR THOMSON.

WITH 92 *ILLUSTRATIONS.*

REVISED EDITION.

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PREFACE

TO THE SECOND EDITION.

THE rapid exhaustion of the large first edition (1889) of this book, and of subsequent reprints also, seems to show the need of a general survey of the essential phenomena of reproduction and sex. That this is in our case associated with a particular theory of the nature of these, need not hinder the reader from discriminating between facts and interpretations. Hence in this revised edition, though many alterations and additions have been made, the original character of the work has been retained, and that notwithstanding the difficulty that the authors have in the past ten years been diverging biologically—the one towards a "Neo-Lamarckian" position, the other towards a "Neo-Darwinian" one. Yet they remain agreed on the main endeavour of the book, which is to set forth the fundamental unity underlying the Protean phenomena of sex and reproduction.

The biological interpretation worked out in this volume may be summarised in three propositions:—

(*A*.) In all living creatures there are two great lines of variation, primarily determined by the very nature of protoplasmic change (metabolism); for the ratio of the constructive (anabolic) changes to the disruptive (katabolic) ones, that is of income to outlay, of gains to losses, is a variable one. In one

sex, the female, the balance of debtor and creditor is the more favourable one; the anabolic processes tend to preponderate, and this profit may be at first devoted to growth, but later towards offspring, of which she hence can afford to bear the larger share. To put it more precisely, the life-ratio of anabolic to katabolic changes, $\frac{A}{K}$, in the female is normally greater than the corresponding life-ratio, $\frac{a}{k}$, in the male. This, for us, is the fundamental, the physiological, the constitutional difference between the sexes; and it becomes expressed from the very outset in the contrast between their essential reproductive elements, and may be traced on into the more superficial secondary sexual characters.

(*B.*) There is much experimental evidence to show that the determining stimuli which cause the balance of life to swing to one side or other, which shunt the plastic organism to this side or to that, are to be found, at least very largely, in the external or environmental conditions—food, temperature, light, chemical media, and so on; so that the determination of sex becomes to some extent practicable in an increasing number of forms.

(*C.*) Yet, the sexual dimorphism, in the main and in detail, has an adaptive significance also, securing the advantages of cross-fertilisation and the like, and is therefore to some extent the result of the continual action of natural selection, though this may of course check variation in one form as well as favour it in another.

So far our main theses. Yet these are obviously but the preliminaries to others. That such an interpretation of the phenomena of sex and reproduction must have its bearing on the whole treatment of the problem of the origin of species is manifest, and it appears to us that these two main variational

lines, upon which we seek to explain the divergent evolution of the sexes, are to be detected also in the variety and the species, in the group and beyond, it may be in the very contrast of plant and animal. But each new mode of interpretation inevitably invites us towards the re-examination of the whole evolutionary process in all its aspects, in all its products. And if, as none now deny, the study of the simpler manifestations of life be a legitimate and even a necessary preliminary to the understanding of human life itself, we must seek fully to rise from our elementary interpretation of reproduction and sex to the study of their vast complexity upon the human plane—anthropological and social, psychological or ethical, educational or practical. We have attempted to indicate some of these considerations more fully in the concluding chapter, as also in some of our separate papers and encyclopædia articles cited in the text, to which a single other reference may be added.* Thus our volume has been from its inception a dozen years ago but the beginning of a larger scheme which its general vastness on one hand, and the pressure of individual duties and cares upon the other, have alike delayed. But though this can never adequately be carried out, we still hope we may be able to do something, together or separately.

The past reception of the book in biological circles has been varied. It has been severely let alone by some authors, even when discussing the subject, and generously borrowed from by others, with or without acknowledgment. It has sometimes completely failed to be understood; we think we may say chiefly by those too pure morphologists to whom our starting-point, the ordinary physiological conception of protoplasmic metabolism as laid down by Claude Bernard

* Cf. the authors "On the Moral Evolution of Sex," THE EVERGREEN, Edinburgh, Summer, 1896.

and his successors, had not been previously familiar. Sometimes too it has been thoughtfully and keenly criticised, and from this we trust we have not wholly failed to profit. But it has also provoked a certain amount of research, which is better than all compliments and criticisms. We venture to think that the general tendency of research has been substantially to confirm, not weaken our general theory: yet our hope is that the growing strength of the still young school of experimental evolutionists may before many years yield results which will involve not merely a revision, but a recasting of our book.

From a wide circle, beyond that of professed biologists, we have also received criticisms suggestive as well as encouraging, and we trust, therefore, that, with all its shortcomings, this revised edition will be found freed of at least some errors, and freshened by the incorporation of some new observations and thoughts.

P. G.
J. A. T.

EDINBURGH,
ABERDEEN, *December*, 1900.

PREFACE

TO THE FIRST EDITION (1889).

IN course of the preparation of critical summaries, such as the articles "Reproduction" or "Sex," contributed by one of us to the "Encyclopædia Britannica," or the account of recent progress annually prepared for the *Zoological Record* by the other, we have not only naturally accumulated considerable material towards a general theory of the subject, but have come to take up an altered and unconventional view upon the general questions of biology, particularly upon that of the factors of organic evolution. Hence this little book has the difficult task of inviting the criticism of the biological student, although primarily addressing itself to the general reader or beginner. The specialist therefore must not expect exhaustiveness, despite a good deal of small type and bibliography, over which other readers (for whose sakes technicalities have also been kept down as much as possible) may lightly skim.

Our central thesis has been, in the first place, to present an outline of the main processes for the continuance of organic life with such unity as our present knowledge renders possible; and in the second, to point the way towards the interpretation of these processes in those ultimate biological terms which physiologists are already reaching as regards the functions of individual life,—those of the constructive and destructive changes (anabolism and katabolism) of living matter or protoplasm.

But while Books I. and II. are thus the more important, and such chapters as "Hermaphroditism," "Parthenogenesis," "Alternation of Generations," have only a subordinate and comparatively technical interest, it will be seen that our theme raises nearly all the burning questions of biology. Hence, for instance, a running discussion and criticism of the speculative views of Professor Weismann, to which their very recent introduction to English readers* has awakened so wide an interest. At once of less technical difficulty, and in some respects even wider issues, is the discussion of Mr Darwin's theory of sexual selection, reopened by the other leading contribution to the year's biological literature which we owe to Mr Alfred Russel Wallace.† Besides entering this controversy at the outset of the volume, we have in the sequel attempted to show that the view taken of the processes concerned with the maintenance of the species leads necessarily to a profound alteration of our views regarding its origin, although the vast problems thus raised necessarily remain open for fuller separate treatment. It is right, however, to say that the restatement of the theory of organic evolution, for which we here seek to prepare (that not of indefinite but definite variation, with progress and survival essentially through the subordination of individual struggle and development to species-maintaining ends), leads us frankly to face the responsibility of thus popularising a field of natural knowledge from which there are so many superficial reasons to shrink, and which knowledge and ignorance so commonly conspire to veil. For if not only the utmost degeneracy be manifestly connected with the continuance of organic species, but also the highest progress and blossoming of life in all its forms, of man or beast or flower, it becomes the first practical

* "Heredity." Oxford, 1889. † "Darwinism." Lond. 1889.

application of biological science not only to investigate and map out these two paths of organic progress, but to illuminate them. Hence we have attempted to indicate the application of the general organic survey, which has been our main theme, to such questions as those of human population and progress, although here, more even than elsewhere, our treatment can be at best only suggestive, not exhaustive. While limits of space have made it impossible to give the botanical side of our subject its proportionate share of attention, our illustrations of the essential facts are sufficient to show the parallelism of the reproductive processes throughout nature.

It remains to express our thanks to Professor F. Jeffrey Bell for some valuable suggestions while the work was passing through the press; to Mr G. F. Scott-Elliot for assistance in summarising certain portions of the literature; and to our engravers, Messrs Harry S. Percy, F. V. M'Combie, and G. A. Morison, especially to the first-named, who has executed the great majority of our illustrations with much care and skill.

PATRICK GEDDES.
J. ARTHUR THOMSON.

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BOOK I.

THE SEXES AND SEXUAL SELECTION.

THE EVOLUTION OF SEX.

CHAPTER I.

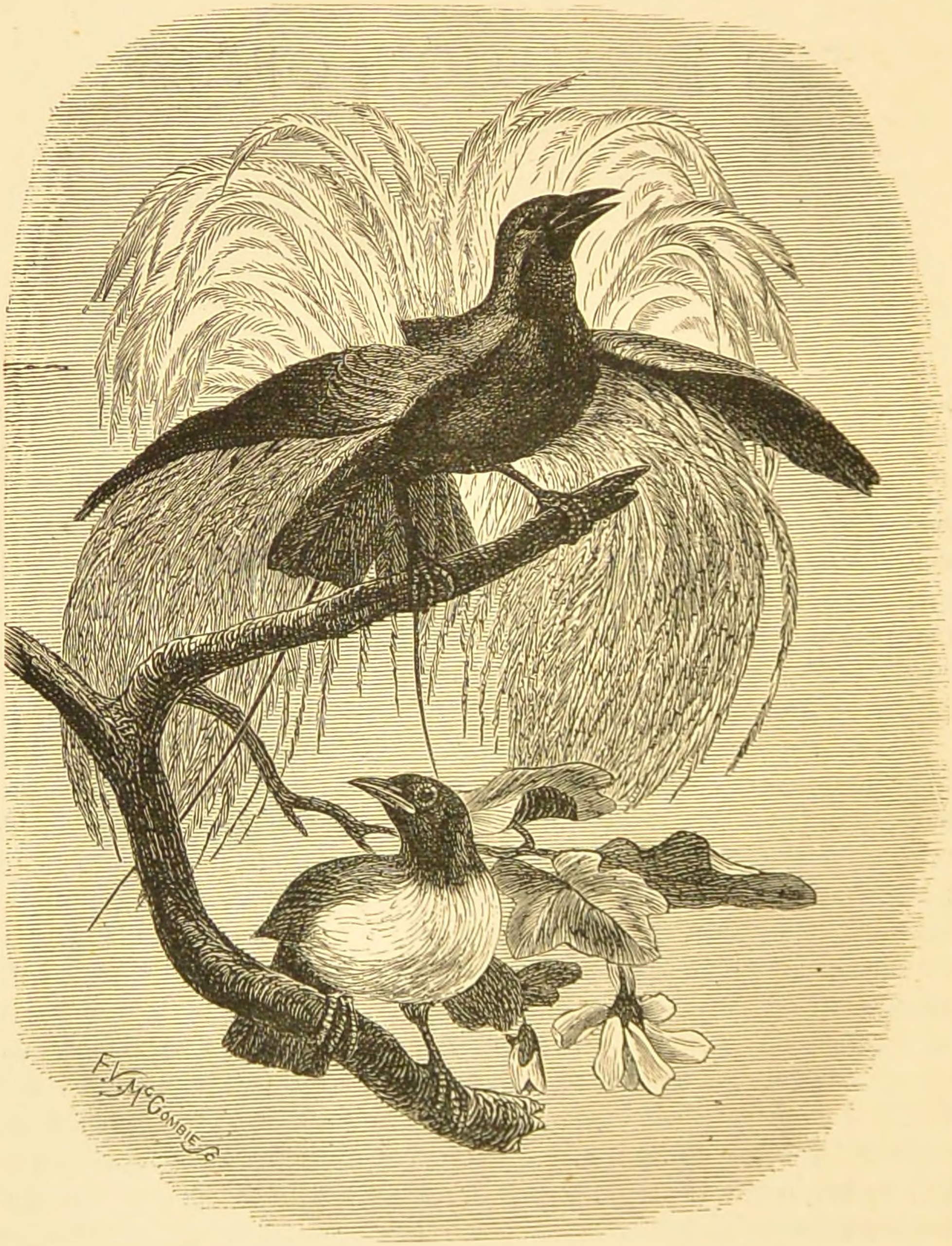
The Sexes and Sexual Selection.

THAT all higher animals are represented by distinct male and female forms, is one of the most patent facts of observation, striking enough in many a beast and bird to catch any eye, and familiarly expressed in not a few popular names which contrast the two sexes. In lower animals, the contrast, and indeed the separateness, of the sexes often disappears; yet even naturalists have sometimes mistaken for different species, what were afterwards recognised to be but the male and female of a single form.

§ 1. *Primary and Secondary Characters.*—When we pass from this commonplace of observation and experience to inquire more precisely into the differences between the sexes, we speedily recognise that these are of very different degrees. In some cases no marked differences whatever are recognisable; thus a male star-fish or sea-urchin looks exactly like the female, and a careful examination of the essential reproductive organs is requisite to determine whether these respectively produce male elements or eggs. In other cases, for instance in most reptiles, no external differences are at all striking, but the aspect of the internal organs, both essential and auxiliary to reproduction, at once settles the question. In a great number of cases, again, the sexes resemble one another closely, but each has certain minor structural features at once decisive as to its respective maleness or femaleness. Thus in the males there are frequently prominent organs used in sexual union, while the peculiar functions of the females are indicated in the special egg-laying or young-feeding organs. All such characters,

directly associated with the essential functions of the sexes, are included under the title of *primary* sexual characters.

Of less real importance, though often much more striking, are the numerous distinctions in size, colour, skin, skeleton, and



Male and Female Bird of Paradise (*Paradisea minor*).—From Catalogue of Zoological Museum, Dresden.

the like, which often signalise either sex. These are termed *secondary* sexual characters; for though they will be shown in

some cases at least to be truly part and parcel with the male or female constitution, they are only of secondary importance in the reproductive process. The beard of man and the mane of the lion, the antlers of stags and the tusks of elephants, the gorgeous plumage of the peacock or of the bird of paradise, are familiar examples of secondary sexual characters in males. Nor are the females lacking in special characteristics, which serve as indices of their true nature. Large size is one of the commonest of these; while in some few cases the excellencies of colour, and other adornments, are possessed by the females rather than by their mates.

The whole subject of secondary sexual characters has found its most extensive treatment in Darwin's "Descent of Man," and to that work, therefore, the more so as its limits exceed those of the present volume, the reader must be assumed to make reference. All that can be here attempted is an illustration, by representative cases, of the main differences between the sexes; from which we shall pass to Darwin's interpretation, and, after a fresh survey, to a re-statement from another point of view.

§ 2. *Illustrations from Darwin.* — Among invertebrates, prominent secondary sexual characters are rarely exhibited outside the great division of jointed-footed animals or arthropods. There, however, among crustaceans and spiders, but especially among insects, beautiful illustrations abound. Thus the great claws of crabs are frequently much larger in the males; and male spiders often differ from their fiercely coy mates, in smaller size, brighter colours, and sometimes in the

Winged Male and Wingless Female of a Moth (*Orgyia antiqua*).—From Leunis.

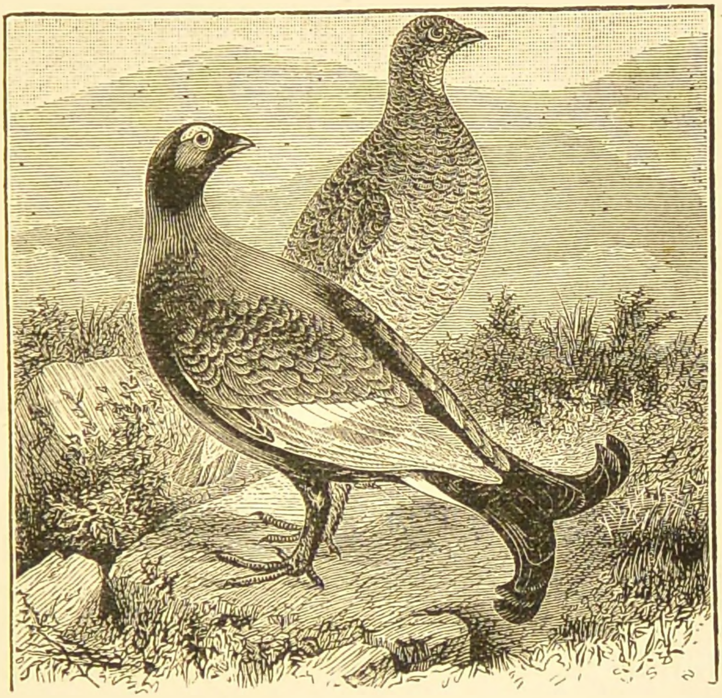
power of producing rasping sounds. Among insects, the males are frequently distinguished by brighter colours attractively displayed, by weapons utilised in disposing of their rivals, and by the exclusive possession of the power of noisy love-calling. Thus, as the Greek observed, the cicadas "live happy, having voiceless wives." Not a few male butterflies are pre-eminently

more brilliant than the females; and many male beetles fight savagely for the possession of their mates.

Passing to backboned animals, we find that among fishes the males are frequently distinguished by bright colours and ornamental appendages, as well as by structural adaptations for combat. Thus the "gemmeous dragonet" (*Callionymus lyra*) is flushed with gorgeous colour, in great contrast to the "sordid" female, and is further adorned by a graceful elongation of the dorsal fin. In many cases, as in the sea-scorpion (*Cottus scorpius*), or in the stickleback (*Gasterosteus*), it is only at the reproductive period that the males are thus transformed, literally putting on a wedding-garment. Every one knows, on the other hand, the hooked lower jaw of the male salmon, which comes to be of use in the furious charges between rivals; and this is but one illustration of many structures utilised in the battle for mates. In regard to amphibians, it is enough to recall the notched crests and lurid colouring of our male newts, and the indefatigable serenading powers of male frogs and toads, to which the females are but weakly responsive. Among reptiles, differences of this sort are comparatively rare, but male snakes have often more strongly-pronounced tints, and the scent-glands become more active during the breeding season. In this, as in many other cases, love has its noisy prayer replaced by the silent appeal of fragrant incense. Among lizards, the males are often more brightly decorated, the splendour of their colours being frequently exaggerated at pairing time. They may be further distinguished by crests and wattle-like pouches; while horns, probably used in fighting, are borne by some male chamæleons.

It is among birds, however, that the organic apparatus of courtship is most elaborate. The males very generally excel in brighter colours and ornaments. Beautiful plumes, elongated feathery tresses, brightly-coloured combs and wattles, top-knots and curious markings, occur with marvellous richness of variety. These are frequently displayed by their possessors before the eyes of their desired mates, with what seem to us like emotions of love and vanity. Or it may be to the subtler charms of music that the wooers mainly trust. During the breeding season, the males are jealously excited and pugnacious, while some have special weapons for dealing directly with their rivals. The differences between the magnificent male birds of paradise and their soberly coloured mates, between the peacock with his hundred

eyes and the plain peahen, between the musical powers of male and female songsters, are very familiar facts. Or again, the combs and "gills" of cocks, the "wattles" of turkey-cocks, the immense top-knot of the male umbrella-bird (*Cephalopterus ornatus*), the throat-pouch of the bustard,—illustrate another

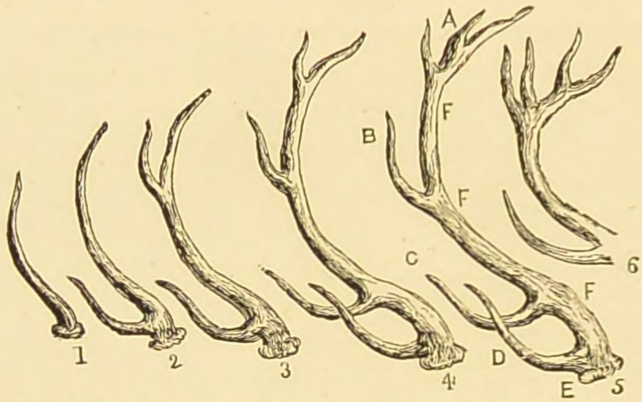


Blackcock and Grey Hen (Male and Female).

series of secondary sexual characters. The spurs of cocks and allied birds are the most familiar illustrations of weapons used by the males in fighting with rivals. As in other animals, it is important to notice that male birds often acquire their special secondary characters, such as colour, markings, and special forms of feathers, only as they approach sexual maturity, and sometimes retain them in all their glory only during the breeding season.

Among mammals, which stand in so many ways in marked contrast to birds, the law of battle much more than the power of charming decides the problem of courtship. Thus most of the striking secondary characters of male mammals are weapons. Yet there are crests and tufts of hair, and other acknowledgments of the beauty test, while the incense of odoriferous glands is a very frequent means of sexual attrac-

tion. The colours too of the males are often more sharply contrasted, and there are minor differences, in voice and the like, which cannot be ignored. Of weapons, the larger canine teeth of many male animals, such as boars; the special tusks of, for instance, the elephant and narwhal; the antlers of stags,



The development of antlers in the successive years of a stag's life, or in the general history of stags.—From Carus Sterne.

all but exclusively restricted to the combative sex; the horns of antelopes, goats, etc.,—which are usually much stronger in the males,—are well-known illustrations. The manes of male lions, bisons, and baboons; the beards of certain goats; the crests along the backs of some antelopes; the dewlaps of bulls,—illustrate another set of secondary characters. The odoriferous glands of many mammals are more developed in the males, and become specially functional during the breeding season. This is well illustrated in the case of goats, deer, shrew-mice, elephants. The differences in colour are slight compared with those seen between the sexes in birds, but in not a few orders the distinction is marked enough, males being, in the great majority of cases, the more strongly and brilliantly coloured. Among monkeys the difference in colour in the bare regions, and the subtler decorations in the arrangement of the hair on the face, are often very conspicuous.

§ 3. *Darwin's Explanation — Sexual Selection.* — Darwin started from the occurrence of such variations, in structure and habit, as might be useful either for attraction between the sexes or in the direct contests of rival males. The possessors of these variations succeeded better than their neighbours in the art of courtship; the factors which constituted success were transmitted to the offspring; and, gradually, the variations were

established and enhanced as secondary sexual characters of the species. The process by which the possessors of the fortunate excellencies of beauty and strength outbid or overcome their less endowed competitors, he termed "sexual selection." It is only fair, however, to state Mr Darwin's case by direct quotation.

Sexual selection "depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction." . . . In cases where "the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone, sexual selection must have come into action." . . . "A slight degree of variability, leading to some advantage, however slight, in reiterated deadly contests, would suffice for the work of sexual selection." . . . So too, on the other hand, the females "have, by a long selection of the more attractive males, added to their beauty or other attractive qualities." . . . "If any man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see no reason to doubt that female birds, by selecting during thousands of generations the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect." . . . "To sum up on the means through which, as far as we can judge, sexual selection has led to the development of secondary sexual characters. It has been shown that the largest number of vigorous offspring will be reared from the pairing of the strongest and best-armed males, victorious in contests over other males, with the most vigorous and best-nourished females, which are the first to breed in the spring. If such females select the more attractive, and at the same time vigorous males, they will rear a larger number of offspring than the retarded females, which must pair with the less vigorous and less attractive males. So it will be if the more vigorous males select the more attractive, and at the same time healthy and vigorous females; and this will especially hold good if the male defends the female, and aids in providing food for the young. The advantage thus gained by the more vigorous pairs in rearing a larger number of offspring, has apparently sufficed to render sexual selection efficient." Another sentence from Darwin's first statement of his position

must, however, be added. "I would not wish," he says in the "Origin of Species," "to attribute all such sexual differences to this agency; for we see peculiarities arising and becoming attached to the male sex in our domestic animals, which we cannot believe to be either useful to the males in battle or attractive to the females."

§ 4. *Criticisms of Darwin's Explanation.* — The above explanation may be summed up in a single sentence,—a congenital variation, advantageous to its possessor (usually a male) in courtship and reproduction, becomes established and perfected by the success it entails. Sexual selection is thus only a special case of the more general process of natural selection, with this difference, that the female for the most part takes the place of the general environment in the picking and choosing which is believed to work out the perfection of the species.

The more serious objections which have been hitherto urged against this hypothesis, apart altogether from criticism of special cases, are the following:—(*a*) Alfred Russel Wallace and others would explain the facts on the more general theory of natural selection, allowing comparatively little import to the alleged sexual selection exercised by the female. (*b*) Some, who allow great importance to both natural and sexual selection, are not satisfied with leaving variation a mere postulate. The position occupied by Brooks will be sketched below. (*c*) Different from either of the above is the position occupied by St George Mivart and others, who attach comparatively little importance to either natural or sexual selection, but seek in terms of definite variation, constitutional tendencies, laws of growth,—for the idea is very variously expressed,—to find the primary and fundamental interpretation of sexual dimorphism.

(*a*) *Wallace's Objection.*—It is convenient to begin with Wallace's early criticism, which precedes that of Brooks in chronological order. This is the more helpful in clearing the ground, since the two theories of Wallace and Darwin are strikingly and, at first sight, irreconcilably opposed. According to Darwin, the gayness of male birds is due to selection on the part of the females; according to Wallace, the plainness of female birds is due to natural selection, which has eliminated those which persisted to the death in being gay. He points out that conspicuousness during incubation would be dangerous and fatal; the more conspicuous have, he thinks, been picked off their nests by hawks, foxes, and the like, and hence only

the sober-coloured females now remain. Darwin starts from inconspicuous forms, and derives gorgeous males by sexual selection; Wallace starts from conspicuous forms, and derives the sober females by natural selection; the former trusts to the preservation of beauty, the latter to its extinction. In 1773, the Hon. Daines Barrington, a naturalist still remembered as the correspondent of Gilbert White, suggested that singing-birds were small, and hen-birds mute for safety's sake. This suggestion Wallace has repeated and elaborated in reference especially to birds and insects. The female butterfly, exposed to danger during egg-laying, is frequently dull and inconspicuous compared with her mate. The original brightness has been forfeited by the sex as a ransom for life. Female birds in open nests are similarly, in many cases, coloured like their surroundings; while in those birds where the nests are domed or covered, the plumage is gay in both sexes.

But in his book on "Darwinism" Wallace goes much further in his destructive criticism of Darwin's sexual selection. The phenomena of male ornament are discussed, and summed up as being "due to the general laws of growth and development," and such that it is "unnecessary to call to our aid so hypothetical a cause as the cumulative action of female preference." Or again, "if ornament is the natural product and direct outcome of superabundant health and vigour, then no other mode of selection is needed to account for the presence of such ornament." This mode of criticism, however, belongs to our third category.

(*b*) Brooks has called attention to the sexual differences in lizards, where the females do not incubate; or in fishes, where the females are even less exposed to danger than the males; or in domesticated birds, where, though all danger is removed, the males are still the more conspicuous and diversified sex. "The fact too that many structures, which are not at all conspicuous, are confined, like gay plumage, to male birds, also indicates the existence of an explanation more fundamental than the one proposed by Wallace, and the latter explanation gives no reason why the females of allied species should often be exactly alike when the males are very different." To the explanation which Brooks proposes we must therefore pass.

According to Darwin, Brooks says, the greater modification of the males is due to their struggling with rivals, and to their selection by the females, but "I do not believe that this goes

to the root of the matter." The study of domesticated pigeons, for instance, shows that "something within the animal determines that the male should lead and the female follow in the evolution of new breeds." The same is true in other domesticated animals, where, from the nature of the circumstances, it is inadmissible to explain this with Darwin, by supposing that the male is more exposed than the female to the action of selection, whether natural or sexual. Darwin concludes, indeed, that the male is more variable than the female, but he gives no satisfactory reason why female variations should be less apt than male variations to become hereditary, or, in other words, why the right of entail is so much restricted to the male sex. Darwin merely attributes this to the greater eagerness of the males, which "in almost all animals have stronger passions than the females." The theory which Brooks maintains, is bound up with an hypothesis of heredity differing considerably from that held by Darwin. He supposes that the cells of the body give off gemmules, chiefly during change of function or of environment, and that "the male reproductive cell has gradually acquired, as its especial and distinctive function, a peculiar power to gather and store up these gemmules." The female reproductive cells keep up the general constancy of the species, the male cells transmit variations. "A division of physiological labour has arisen during the evolution of life, and the functions of the reproductive elements have become specialised in different directions." "The male cell became adapted for storing up gemmules" (the results of variations in the body), "and at the same time gradually lost its unnecessary and useless power to transmit hereditary characteristics." "We thus look to the cells of the male body for the origin of most of the variations through which the species has attained to its present organisation." The males are the more variable, but more than that, their variations are much more likely to be transmitted. "We are thus able to understand the great difference in the males of allied species, the difference between the adult male and the female or young, and the great diversity and variability of secondary male characters; and we should expect to find, what actually is the case, that among the higher animals, when the sexes have long been separated, the males are more variable than the females." The contrast between Darwin and Brooks may now be summed up again in a sentence. Darwin says,

the males are more diversified and richer in secondary sexual characters, chiefly because of the sexual selection exercised alike in courtship and in battle. Brooks admits sexual selection, but believes that the males are naturally or constitutionally more variable than the females, and that it is the peculiar function of the male elements to transmit variations, as opposed to the constant tradition of structure kept up by the egg-cells or ova. In other words, the females may choose, yet the males lead; nay more, they must lead, for male variations have by hypothesis most likelihood of being transmitted.

Full consideration of this hypothesis would involve much discussion of the problems of inheritance, but the general conclusion of the naturally greater variability of the males, will be stated in a different light towards the close of the following chapter. It will there be shown that the "something within the animal," which determines the preponderance of male variability, may be stated in simpler terms than are involved in Brooks's theory. Moreover, the greater variability of the males, which seems quite plain when we contrast, for instance, ruffs and reeves, requires to be proved for each case. Karl Pearson has disproved it for man.

Somewhat similar to Wallace's *later* position is that (*c*) occupied by St George Mivart, who also looks for some deep constitutional reason for sexual dimorphism. The entire theory of sexual selection appears to him an unverified hypothesis, only acquiring plausibility when supported by numerous subsidiary suppositions. He submits a number of detailed criticisms; but his chief contention is, that the beauty of males, and other secondary sexual characters, are not the indirect results of a long process of external selection, but the direct expressions of the internal differences of a progressively varying internal constitution, *i.e.*, of tendencies inherent in the individual.

Mivart's position and the vague suggestions of Mantegazza and others are of importance as indications of progress towards a fundamental re-statement. As we have seen, an obvious objection to the theory of sexual selection is that, while it may in part account for the persistence and progress of secondary characters after they attained a certain degree of development, it does not account for their preservation when weak or inconspicuous. In short, the theory may account for the perfecting, but not for the origin of the characters. It may be enough to

account for the length and the trimmings of the living garment, but what we wish to know is the secret of the loom. Darwin's account of the evolution of the eyes on the feathers of the Argus pheasant is indeed ingenious and interesting; but, whatever its probability, it is more important to ask what the predominant brightness of males means as a general fact in physiology. It is of interest, then, to notice the hints thrown out by Mantegazza, Wallace, and others, directly associating decorativeness with superfluous reproductive material, and the putting on of wedding-robes with the general excitement of the sexually mature organism. From this record of the discussion, it is time however to turn to a more constructive mode of treatment.

In passing, however, it should be noted that the fact of preferential or selective mating can be proved not only by observation, as the Peckhams have done in the case of spiders, but more conclusively by statistical enquiry, by investigating "whether the type and variability of the mated and unmated members of one or other sex are the same" (see Karl Pearson's "Grammar of Science," 2nd ed., 1900, p. 425). Apart from the particular problem of secondary sexual characters, it is of the utmost importance whether the mating is selective or indiscriminate. For if natural selection is at work its effect will be checked by indiscriminate mating, and aided by preferential or, to use the wider term, selective mating.

SUMMARY.

1, 2. The existence of male and female animals is a commonplace of observation. They differ in primary and in secondary sexual characters, of which illustrations are given, chiefly from Darwin.

3. Darwin's theory of sexual selection seeks to account for the preservation and perfection of variations, advantageous in courtship or in battles with rivals.

4. Wallace maintains that the females have been protectively retarded by natural selection, and at a later date suggests that the greater decorativeness, etc., of the males is an expression of superabundant vigour. Brooks believes that the males are naturally the more variable, and predominate in power of transmitting variations. Mivart demands a deeper analysis than is afforded by either sexual or natural selection. This physiological rationale is hinted at.

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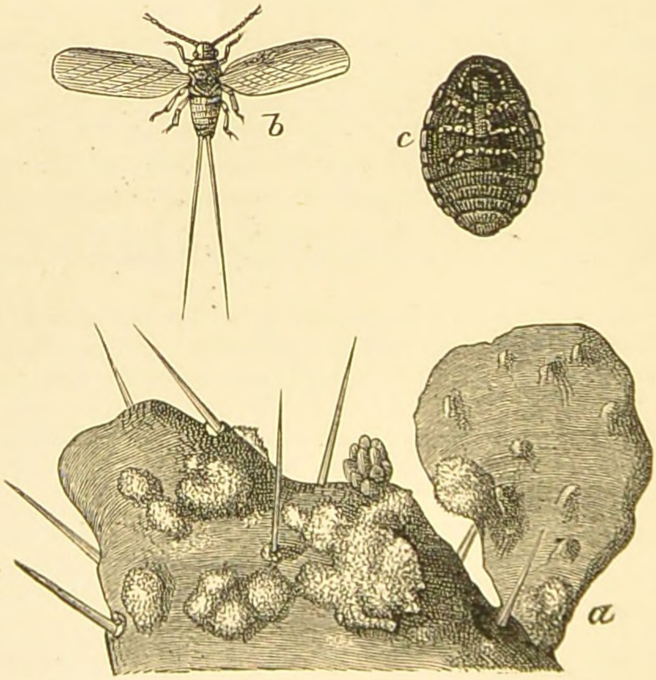
CHAPTER II.

The Sexes, and Criticism of Sexual Selection.

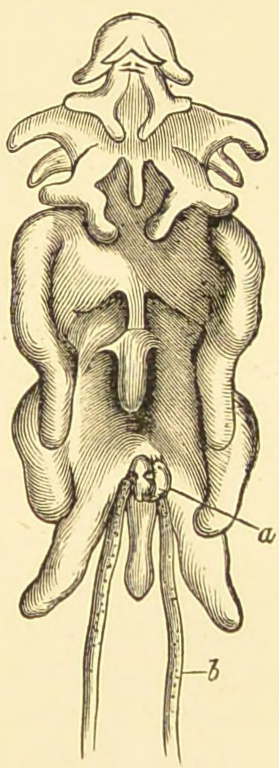
§ 1. *Sex-Differences.*—To gain a firmer and broader foundation on which to base a theory of the differences between the sexes, it is necessary to take another review of the facts of the case. Instead of considering the differences as they are expressed in the successive classes of animals, it will be more convenient to arrange them for themselves, according as they affect habit, size, length of life, and the like. The review must again be merely representative, without any attempt at completeness.



Male and Female Coccus Insects. *a*, part of a cactus plant with the excrescences due to coccus insects; *b*, male; *c*, female.

§ 2. *General Habit.*—Let us begin with an extreme yet well-known case. The female cochineal insect, laden with carmine, which some have interpreted as a reserve-product, spends

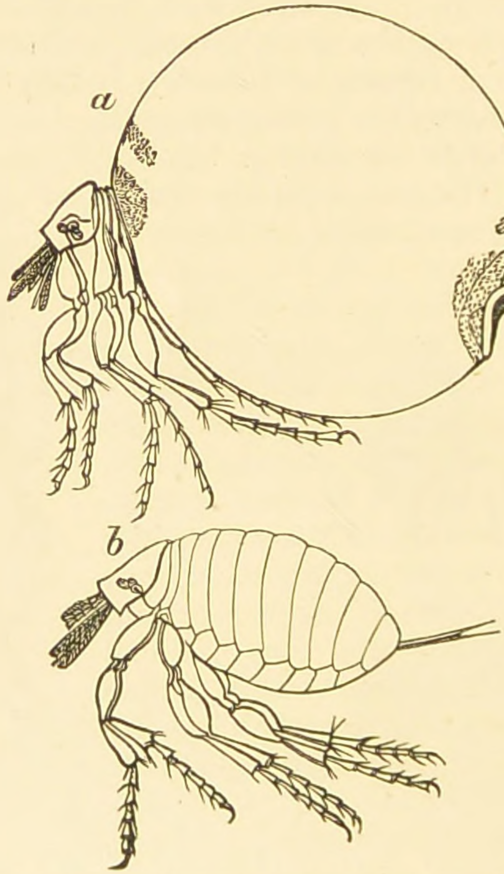
much of its life like a mere quiescent gall on the cactus plant. The male, on the other hand, in his adult state is agile, restless, and short-lived. Now this is no mere curiosity of the entomologist, but in reality a vivid emblem of what is an average truth throughout the world of animals—the preponderating passivity of the females, the predominant activity of the males. These coccus insects are the martyrs of their respective sexes. Take another illustration, again somewhat extreme. There is a troublesome threadworm (*Heterodera schachtii*) infesting the turnip plant, which parallels in more ways than one the contrast of the coccus insects. The adult male is agile, and like many another threadworm; the adult female, however, is quiescent, and bloated like a drawn-out lemon. It may be asked, however, is not this merely the natural nemesis of parasitism? The life-history answers this objection. The two sexes are at first alike,—agile, and resembling most threadworms; they become parasitic, and lose both activity and nematode form; but the interesting fact is further, that the male recovers himself, while the female remains a victim. In other insect and worm types the same story, in less accented characters, may be distinctly read. In many crustaceans, again, the females only are parasitic; and while this is in part explained by their habit of seeking shelter for egg-laying purposes, it also expresses the constitutional bias of the sex. The insect order of bee parasites (Strepsiptera) is remarkable for the completely passive and even larval character of the blind parasitic females, while the adult males are free, winged, and short-lived. Throughout the class of insects there are numerous illustrations of the excellence of the males over the females, alike in muscular power and sensory acuteness. The diverse series of efforts by which the males of so many different animals, from cicadas to birds, sustain the love-chorus, affords another set of illustrations of pre-eminent masculine activity.



Female *Chondracanthus*, a parasitic Crustacean, with pigmy male (*a*) attached just above the origin of the long egg-sacs (*b*) of the female. —From Claus.

Without multiplying instances, a review of the animal

kingdom, or a perusal of Darwin's pages, will amply confirm the conclusion that on an average the females incline to passivity, the males to activity. In higher animals, it is true that the contrast shows rather in many little ways than in any one striking difference of habit, but even in the human species the contrast is recognised. Every one will admit that strenuous spasmodic bursts of activity characterise men, especially in youth, and among the less civilised races; while patient continuance, with less violent expenditure of energy, is as generally associated with the work of women.



Both sexes of a Flea—the Jigger or Chigoe (*Sarcopsylla penetrans*); the female much swollen with eggs.—From Leuckart.

For completeness of argument, two other facts, which will afterwards claim full discussion, may here be simply mentioned. (*a*) At the very threshold of sex-difference, we find that a little active cell or spore, unable to develop of itself, unites in fatigue with a larger more quiescent individual. Here, at the very first, is the contrast between male and female. (*b*) The same antithesis is seen, when we contrast, as we shall afterwards

do in detail, the actively motile, minute, male element of most animals and many plants, with the larger passively quiescent female-cell or ovum.

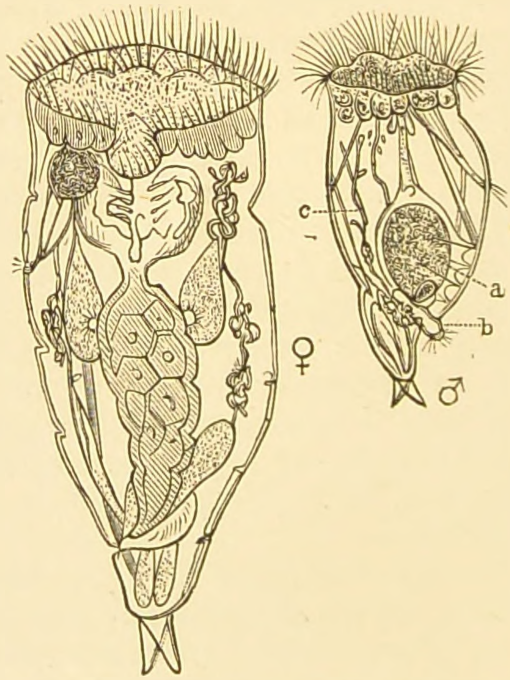
It is possible that the reader may urge as a difficulty against the above contrast the exceedingly familiar case of the male bees or "drones." It must be frankly allowed that exceptions do indeed occur, though usually in conditions which afford a key to the abnormality. Thus it will be allowed that the "drones" are in a peculiar position as male members of a very complex society, in which what is practically a third sex is represented by the great body of "workers." They are no more fair examples of the natural average of males, than the hard-driven wives of the lazy Kaffir are of the normal functions of women. Nor is the exception even here a real one, for the drone, although passive as compared with the unsexed workers, is active when compared with the extraordinarily passive queen.

To the above contrast of general habit, two other items may be added, on which accurate observation is still unfortunately very restricted. In some cases the body temperature, which is an index to the pitch of the life, is distinctly lower in the females, as has been noted in cases so widely separate as the human species, insects, and plants. In many cases, furthermore, the longevity of the females is much greater. Such a fact as that women pay lower insurance premiums than do men, is often popularly accounted for by their greater immunity from accident; but the greater normal longevity on which the actuary calculates, has, as we begin to see, a far deeper and constitutional explanation.

§ 3. *Size.*—Among the higher animals, there are curious alternations in the preponderance of one sex over another in size. Thus among mammals and birds the males are in most cases the larger; the same is true of lizards; but in snakes the females preponderate. In fishes, the males are on an average smaller, sometimes very markedly so, even to the extent of not being half as large as their mates. Below the line, among backboneless animals, there is much greater constancy of predominance in favour of the females. Thus among insects, the more active males are generally smaller, and often very markedly; of spiders the same is true, and the males being often very diminutive are forced to task their agility to the utmost in making advances to their unamiable mates. So again, crustacean males are often smaller than the females; and

in many parasitic species, what have been well called "pigmy" males illustrate the contrast in an almost ludicrous degree.

Two cases from aberrant worm types exhibit very vividly this same antithesis of size. Among the common rotifers, the males are almost always very different from the females, and much smaller. Sometimes they seem to have dwindled out of existence altogether, for only the females are known (*Philodina*, *Rotifer*, *Callidina*, *Adineta*). In *Polyarthra platyptera* the male is "hardly to be distinguished from a *Vorticella* which has become detached from its stalk." In *Hydatina senta* (see fig.) the male is about a third the size of the female, has no alimentary canal, and has only two or three days of adult life. In the great majority the males are "little more than perambulating bags of spermatozoa," though in a few cases, like *Rhinops vitrea*, degeneration seems hardly to have begun (Rousselet, 1897). Even when present, they are not indispensable, for parthenogenesis is very general.



Relative sizes of a male and female Rotifer (*Hydatina senta*).
—From Leunis.

In a remarkable marine worm, *Bonellia*, the male remains like a remote ancestor of the female. It lives parasitically on or within the latter, and is microscopic in size, measuring in fact only about one hundredth part of the length of its host and mate. Somewhat similar to the case of *Bonellia* is that of a viviparous coccus insect (*Lecanium hesperidum*), where the males are very degenerate, small, blind, and wingless. In spite of this condition, perhaps indeed because of it, they are very

male, for even the larvæ, while still within the mother, have been shown to contain fully-developed spermatozoa. In a little "bear animalcule" or Tardigrade, *Macrobiotus macronyx*, the males are about half the size of the females and decidedly more active. A particularly interesting case of sexual dimorphism in molluscs has been described by Professor E. G. Conklin ("Proc. Acad. Nat. Sci. Philadelphia," 1898, pp. 435-444, 3 pls.). In *Crepidula plana*, which occurs in

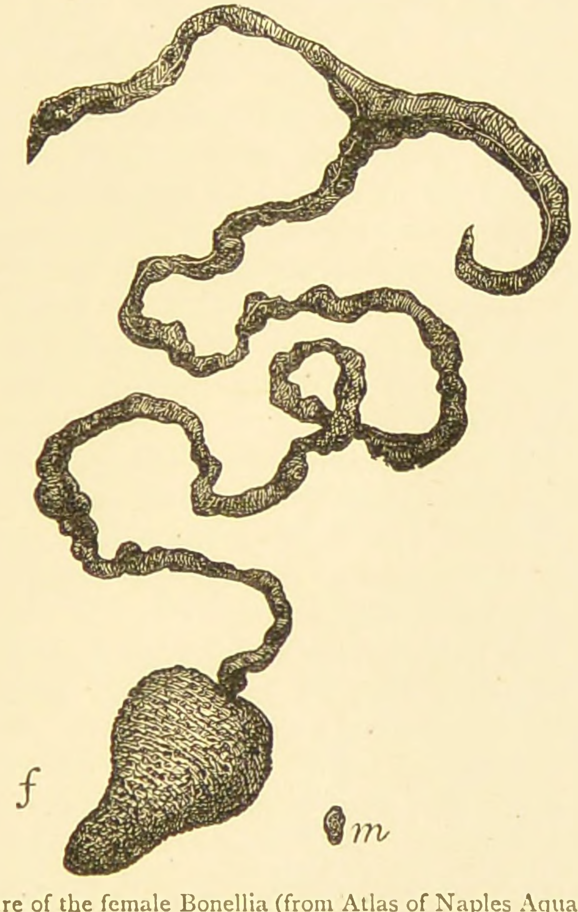


Figure of the female Bonellia (from Atlas of Naples Aquarium), with its parasitic pigmy male enlarged.

shells tenanted by hermit-crabs (*Eupagurus bernhardus*), the female is about fifteen times larger than the male, and the latter retains throughout life the power of locomotion possessed by the females in their young stages only. The females occurring along with the little hermit-crab, *Eupagurus longicarpus*, are always dwarfed, having a body volume only one-thirteenth of the more typical form. The cells of the dwarfs are of the normal size, but there are fewer of them, and

the eggs are also much less numerous. But this dwarfing is a mere "modification," and not inherited; it probably depends upon pressure or upon differences of nutrition and oxygenation. That is to say, the dwarfs are not a race, but are continually recruited from the young of the giants. It is interesting, therefore, to note that environmental influences may modify the female till in size it resembles the normally dwarfish male; and that the small size of the male implies, as in the case of the dwarfs, not smaller cells, but a smaller number of cells. In both dwarfs and males, the process of cell-division has been inhibited.

Dr T. W. Fulton, Naturalist to the Scottish Fishery Board, has made valuable statistical observations on the size and numerical proportions of male and female fishes. (1) The females are usually considerably more numerous than the males, and never less numerous except in the angler and the cat-fish. The proportion of females to males among flat-fishes ranges from about 1 : 1 in the flounder, to about 12 : 1 in the long rough dab. Among "round" fishes the same proportion varies from about 3 : 2 in the cod, to 9 : 2 in the common gurnard. (2) The female is longer and larger among all the flat-fishes, sometimes by as much as 30 per cent. In cod, haddock, angler, and cat-fish, the males are larger, while in the whiting the females are slightly larger, and in the common gurnard decidedly so.

One must not indeed base an argument on extreme cases, but there is no doubt that up to the level of amphidians at least the females are generally the larger.

Apparent exceptions occur, it is true, among the higher animals. In birds and mammals the males are usually rather larger than the females. This difference consists especially in larger bones and muscles. The apparent exception is in part the natural result of the increased stress of external activities which are thrown upon the shoulders of the males when their mates are incapacitated by incubation or pregnancy. Furthermore, we must recognise the strengthening influence of the combats between males, and the effect produced on the accumulative constitution of the females by the increased maternal sacrifice characteristic of the highest animals.

§ 4. *Other Characters.*—While it is easy to point to the general physiological import of large size and the reverse, physiology is not yet far enough advanced to afford firm foot-

hold in dealing with the details of secondary sexual characters. It is only possible to point out the path which will eventually lead us to their complete rationale. The point of view is simple enough. The agility of males is not merely an adaptation to enable that sex to exercise its functions with relation to the other, but is a natural characteristic of the constitutional activity of maleness; and the small size of many male fishes is not an advantage at all, but simply again the result of the contrast between the more vegetative growth of the female and the costly activity of the male. So, brilliancy of colour, exuberance of hair and feathers, activity of scent-glands, and even the development of weapons, cannot be satisfactorily explained by sexual selection alone, for this is merely a secondary factor. In origin and continued development they are outcrops of a male as opposed to a female constitution. To sum up the position in a paradox, all secondary sexual characters are at bottom primary, and are expressions of the same general habit of body (or to use the medical term, *diathesis*), as that which results in the production of male elements in the one case, or female elements in the other. This theory of the origin and primary meaning of those variations which culminate in marked sexual dimorphism is obviously similar to that adopted by Wallace in his book on "Darwinism."

Three well-known facts must be recalled to the reader's mind at this point; and firstly, that in a great number of cases the secondary sexual characters make their appearance step by step with sexual maturity itself. When the animal—be it a bird or insect—becomes emphatically masculine, then it is that these minor outcrops are exhibited. Thus the male bird of paradise, eventually so resplendent, is usually in its youth comparatively dull and female-like in its colouring and plumage. Very often, too, whether in the wedding-robe of male fishes or in the scent-glands of mammals, the character rises and wanes in the same rhythm as that of the reproductive periods. It is impossible not to regard at least many of the secondary sexual characters as part and parcel of the sexual diathesis,—as expressions for the most part of exuberant maleness.

Secondly, when the reproductive organs are removed by castration, the secondary sexual characters are often much modified. Thus, as Darwin notes, stags never renew their

antlers after castration, though normally, of course, they renew them each breeding season. The reindeer, where the horns occur on the females as well, is an interesting exception to the rule, for after castration the male still renews the growth. This however merely indicates that the originally sexual characters have become organised into the general life of the body. In sheep, antelopes, oxen, &c., castration modifies or reduces the horns; and the same is true of odoriferous glands. The parasitic crustacean *Sacculina* has been shown by Delage to effect a partial castration of the crabs to which it fixes itself, and the same has been observed by Giard in other cases. In two such cases an approximation to the female form of appendage has been observed. Rörig (1899) has shown that a diseased state of the ovaries in deer is correlated with a development of antlers, that atrophy of the testes is always followed by some peculiarity in the antler-growth, that castration of a young male always inhibits the development of antlers, and so on. Sellheim (1898, 1899) finds that in many animals of both sexes castration is followed by a prolongation of the period of bone-growth. In the case of young cocks the effects of castration are very variable, sometimes increasing, sometimes decreasing the secondary sex characters. One result is clear, however, that the whole body is affected; the larynx is intermediate in size between that of cock and hen, the syrinx is weakly developed and the capons seldom crow or do so abnormally, the brain and heart are light in weight, fat accumulates in the subcutaneous and subserous connective tissue, and the skeleton shows many abnormalities. The experiments of J. Th. Oudemans (1898) on castrating caterpillars—a difficult operation—led him to the conclusion, in marked contrast to the above, that there was little result either on the external appearance or on the habits of the adults.

Thirdly, it should also be noted that in aged females, which have ceased to be functional in reproduction, the minor peculiarities of their sex often disappear, and they become liker males, both in structure and habits,—witness the familiar case of "crowing hens."

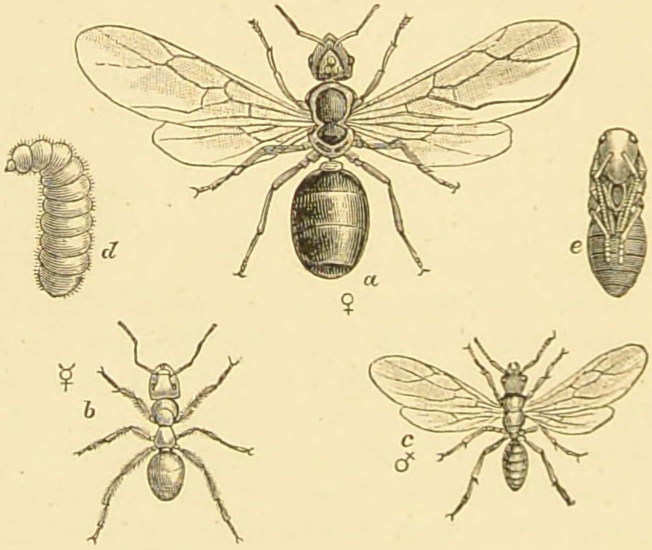
From the presupposition, then, of the intimate connection between the sexuality and the secondary characters (which is indeed everywhere allowed), it is possible to advance a step further. Thus in regard to colour, that the male is usually brighter than the female is an acknowledged fact. But pig-

ments of many kinds are physiologically regarded as of the nature of waste products. Such for instance is the guanin, so abundant on the skin of fishes and some other animals. Abundance of such pigments, and richness of variety in related series, point to pre-eminent activity of chemical processes in the animals which possess them. Technically expressed, abundant pigments are expressions of intense metabolism. But predominant activity has been already seen to be characteristic of the male sex; these bright colours, then, are often natural to maleness. In a literal sense animals put on beauty for ashes, and the males more so because they are males, and not primarily for any other reason whatever. We are well aware that, in spite of the researches of Krukenberg, Sorby, MacMunn, Newbigin, and others, our knowledge of the physiology of pigments is still very scanty. Yet in many cases, alike among plants and animals, pigments are expressions of disruptive processes, and are of the nature of waste products; and this general fact is at present sufficient for our contention, that bright colouring or rich pigmenting is more characteristic of the male than of the female constitution.

In the same way, the skin eruptions of male fishes at the spawning season seem more pathological than decorative, and may be directly connected with the sexual excitement. One instance of the way in which the reproductive maturity is known to effect a by no means obviously related result may be given. Every field naturalist knows that the male stickleback builds a nest among the weeds, and that he weaves the material together by mucous threads secreted from the kidneys. The little animal is also known to have strong passions; it is polygamous in relation to its mates, and most pugnacious in relation to its rivals. Professor Möbius has shown that the male reproductive organs (or testes) become very large at the breeding season, and that they press in an abnormal way upon the kidneys. This encroachment produces a pathological condition in the kidneys, and the result is the formation of a mucous secretion, somewhat similar to what occurs in renal disease in higher forms. To free itself from the irritant pressure of this secretion, the male rubs itself against external objects, most conveniently upon its nest. Thus the curious weaving instinct does not demand or find rationale in the cumulative action of natural selection upon an inexplicable variation, but is traced back to a pathological and mechanical origin in the emphatic maleness of the organism.

The line of variation being thus given, it is of course conceivable that natural selection may have accelerated it.

So too, though again the physiological details are scanty, the superabundant growth of hair and feathers may be interpreted, in some measure through getting rid of waste products, for we shall see later how local katabolism favours cell multiplication. Combs, wattles, and skin excrescences point to a predominance of circulation in the skin of the feverish males, whose temperatures are known in some cases to be decidedly higher than those of the females. Even skeletal weapons like antlers may be similarly interpreted; while the exaggerated activity of the scent-glands is another expedient for excreting waste.



Male (*c*), Worker (*b*), and Queen (*a*) Ant.—From *Chambers's Encyc.*, after Lubbock.

In regard to horns, feathers, and the like, in association with vigorous circulation, two sentences from Rolph may be quoted:—"The exceedingly abundant circulation, which periodically occurs in the at first soft frontal protuberances of stags, admits and conditions the colossal development of horn and delicate ensheathing velvet. . . . In the same way, the rich flow of blood in the feather papillæ conditions the immense growth of the feathers, . . . and the same is true of hairs, spines, and teeth."

Professor J. Kennel gives expression in an interesting essay to an entirely different interpretation of such structures as antlers. It may be that they, like the horns of Ruminants, were originally possessed by both sexes, and that they have been lost by the females whose reproductive sacrifice leaves, as it were, less to spare for such expensive structures as antlers are. So it may be that the female deer have ceased to develop antlers except where the conditions of life rendered their retention indispensable, namely, in the reindeer. In other words, this may be one of the many cases in which the female is nearer not to the ancestral but to the youthful type.

Some of the even subtler differences between the sexes are of interest in illustrating the general antithesis. Thus in the love-lights of the Italian glow insect (*Luciola*), the colour is said to be identical in the two sexes, and the intensity is much the same. That of the female, however, who is in other respects rather male-like in her amatory emotions, is more restricted. It is interesting further to notice that the rhythm of the light in the male is more rapid and the flashes are briefer, while that of the female is longer and the flashes more distant and tremulous. This illustration may thus serve as a literally illumined index of the contrasted physiology of the sexes.

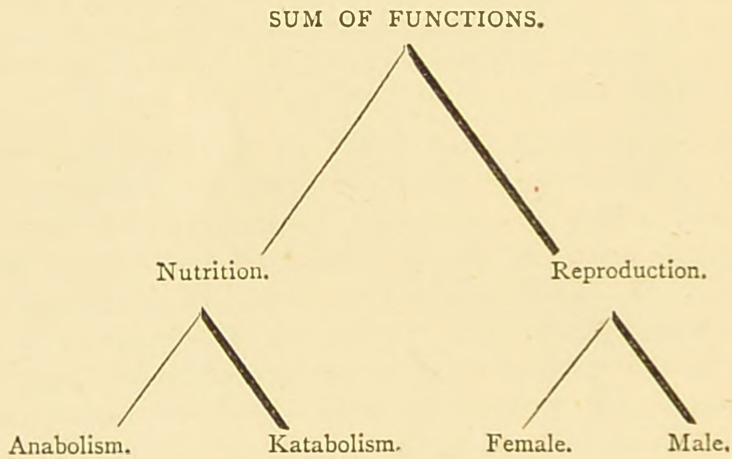
The case of the Psychidæ among Lepidoptera is particularly instructive. Both males and females are normal caterpillars, but while the males become winged, the female remains at the larval level, as regards absence of wings and the usual adult appendages, oral as well as locomotor, but differing from the larva in being reproductive. In short, the female degenerates to the juvenile level except in productivity, while the male without doubt is nearer the ancestral form.

§ 5. *Sexual Selection: its Limit as an Explanation.*—We are now in a better position to criticise Mr. Darwin's theory. On his view, males are stronger, handsomer, or more emotional, because ancestral forms happened to become so in a slight degree. In other words, the reward of breeding-success gradually perpetuated and perfected a casual advantage. According to the present view, males are stronger, handsomer, or more emotional, simply because they are males,—*i.e.*, of more active physiological habit than their mates. In phraseology which will presently become more intelligible and concrete, the males tend to live at a loss, are relatively more *katabolic.* The females, on the other hand, tend to live at a profit, are relatively more *anabolic*,—constructive processes predominating in their life, whence indeed the capacity of bearing offspring.

No one can dispute that the nutritive, vegetative, or self-regarding processes within the plant or animal are opposed to the reproductive, multiplying, or species-regarding processes, as income to expenditure, or as building up to breaking down. But within the ordinary nutritive or vegetative functions of the body, there is necessarily a continuous antithesis between two sets of processes,—constructive and destructive metabolism. The contrast between these two processes is seen throughout nature, whether in the alternating phases of cell life, or of

activity and repose, or in the great antithesis between growth and reproduction; and it is this same contrast which we recognise as the fundamental difference between male and female. The proof of this will run through the work, but our fundamental thesis may at once be roughly enunciated in a diagrammatic expression (which in its present form we owe to our friend Dr W. E. Fothergill):—

Here the sum-total of the functions are divided into nutritive and reproductive, the former into anabolic and katabolic processes, the latter into male and female activities,—so far with all physiologists, without exception or dispute.* Our special theory lies, however, in suggesting the parallelism of the two sets of processes. Thus maleness is associated with a life-ratio in which katabolism has a relatively greater



predominance than in the female. In terms of this thesis, therefore, both primary and secondary sexual characters express the fundamental physiological bias characteristic of either sex. Sexual selection resembles artificial selection, but the female takes the place of the human breeder; it resembles natural selection, but the selective females and the combative

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* The reader whose physiological studies may not have familiarised him with that conception (really dating from Claude Bernard) of all physiological processes as finding their ultimate expression in the metabolism (anabolism and katabolism) of protoplasm, will easily place himself in a position to check our argument (often indeed, we trust to carry our interpretation of sex into still further detail) by starting from the exposition of this doctrine in Sir Michael Foster's article, "PHYSIOLOGY," in the *Encyclopædia Britannica*, or with Sir Burdon Sanderson's Presidential Address to Section D, British Association, 1889.

males represent a rôle filled in the larger case by the fostering or eliminating action of the environment. As a special case of natural selection, Darwin's theory is open to the objection of being teleological, *i.e.*, of accounting for structures in terms of a final advantage. It is also open to the logical critic to urge that the structures to be explained have to be accounted for before, as well as after, the stage when they were developed enough to be useful. The origin, or in other words the fundamental physiological import, of the structures must be explained before we have a complete or adequate theory of organic evolution.

Apart from this logical insufficiency, the theory of sexual selection is open to many minor objections, with some of which Darwin himself dealt. One detailed objection which seems serious may be noticed. The evolution of coloured markings by selective preference carries with it the postulate of a certain level of æsthetic taste and critical power in the female, and this not only very high and very scrupulous as to details, but remaining permanent as a standard of fashion from generation to generation,—large assumptions all, and scarcely verifiable in human experience. Yet we cannot suppose that Mr Darwin considered the human female as peculiarly undeveloped. It is true, doubtless, that both insects and birds have so far and increasingly become educated in such sensitiveness; but when we consider the complexity of the markings of the male bird or insect, and the slow gradations from one stage of perfection to another, it seems difficult to credit birds or butterflies with a degree of æsthetic development exhibited by no human being without both special æsthetic acuteness and special training. Moreover, the butterfly, which is supposed to possess this extraordinary development of psychological subtlety, will fly naïvely to a piece of white paper on the ground, and is attracted by the primary æsthetic stimulus of an old-fashioned wall-paper, not to speak of the gaudy and monotonous brightness of some of our garden flowers. Thus we have the further difficulty, that we must suppose the female butterfly to have a double standard of taste, one for the flowers which she and her mate both visit, the other for the far more complex colouring and markings of the males. And even among birds, if we take those unmistakable hints of real awakening of the æsthetic sense which are exhibited by the Australian bowerbird or by the common

jackdaw in its fondness for bright objects, how very rude is this taste compared with the critical examination of infinitesimal variations of plumage on which Darwin relies. Is not, therefore, his essential supposition too glaringly anthropomorphic?

Again, the most beautiful males are often extremely combative; and on the conventional view this is a mere coincidence, yet a most unfortunate one for Mr Darwin's view. Battle thus constantly decides the question of pairing, and in cases where, by hypothesis, the female should have most choice, she has simply to yield to the victor. On our view, however, combative energy and sexual beauty rise *pari passu* with male katabolism.

Or again, in the *Æneas* group of the genus *Papilio*, Darwin notes how there are frequent gradations in the amount of difference between the sexes. Sometimes the sexes are alike dull, where we should have to suppose the æsthetic perception must somehow have been lost or inhibited; sometimes the females are dull and the males splendid,—for Darwin, an example of the result of sexual æsthetic perception, this of an exquisitely subtle kind however, and without proportionate cerebral enlargement. In a third set of cases, both sexes are splendid, which would suggest logically that the male in turn had acquired a taste for splendour. But such cases, which usually need more or less cumbrous additional hypothesis of inheritance and so on to explain them, are intelligible enough if we regard them as a relative increase of katabolism in the life-ratio throughout a series of species. The third set may be supposed to be relatively more katabolic than the first, while the second set are midway; although, it may be freely granted, a knowledge of the habits, size, &c., of the particular species, would be necessary to verify the legitimacy of this interpretation in each case.*

It is necessary once more to turn to the contrast between the positions of Darwin and Wallace. According to Darwin, sexual selection has accelerated the males into gay colouring;

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* For a discussion of the progressive development of colouring and markings, whether in butterflies or mammals, the reader may be referred to the works of Professor Eimer, especially to his work on Lepidoptera. Reference should also be made to Weismann's "Studies in the Theory of Descent," for a discussion of the markings of caterpillars and butterflies.

according to Wallace's original view, natural selection has retarded the females (birds or butterflies) and kept them inconspicuously plain. It is no longer difficult to establish a compromise. Both sexes have differentiated towards their respective goals, not along lines of indefinite variation, but on paths determined by the characteristic constitutions. In other words, the secondary dimorphism has a definite physiological basis in the primary sex-difference. If this interpretation of the origin of the variants be granted, it remains a matter of observation, experiment, and statistics to determine how far the limits are fixed by natural selection (in Wallace's cases), or by sexual selection (in Darwin's). The present position allows the efficacy of natural and sexual selection as limiting, eliminating, in a sense directive, factors, but regards gay colouring as the expression of the relative predominance of katabolism in the male sex, and quiet plainness as equally natural to the predominantly anabolic females.

At a later stage something more will be said of natural selection, and its limits as an explanation of facts. But it is here desirable to emphasise, that just as we admit the importance of sexual selection as a minor accelerant in the differentiation of the sexes, so we are bound to recognise that natural selection is also continually in operation as a check to a divergence of the sexes which would otherwise tend to become extreme. If this retarding influence of natural selection on the evolutionary process were not continually present, we should find cases like *Bonellia* and the rotifers much commoner than they are among animals. But it is an error to exaggerate this limiting action into an explanation of the process itself.

SUMMARY.

1-3. A broader basis must be sought from which to understand the differences between the sexes. A general survey shows that the males are more active in habit, the females more passive; that the males tend to be smaller and to have a higher body-temperature, while the females tend to be larger and to live longer.

4. The close association of secondary sexual characters with the reproductive function is shown in the period or in the periodicity of their development, in the effects of castration, in the peculiarities of aged females, &c. Richer pigmentation, and other male characteristics, may be interpreted as expressions of the relative katabolic predominance in the constitution of males, as opposed to the relative anabolic preponderance of the females.

5. Sexual selection, as an explanation of secondary sexual characters, does not account for origins nor incipient stages, postulates subtle æsthetic sensitiveness, and is beset by numerous minor difficulties. Yet the opposed positions of Darwin and Wallace both emphasise indubitable facts; while the criticisms of Mivart, the theory of Brooks, and the suggestions of Rolph, Mantegazza, and others, lead on towards a deeper analysis. The general conclusion reached, recognises sexual selection (so far with Darwin) as a minor accelerant, natural selection (so far with Wallace) as a retarding "brake," on the differentiation of sexual characters, which essentially find a constitutional or organismal origin in the relatively katabolic or anabolic diathesis which characterises males and females respectively.

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CHAPTER III.

The Determination of Sex (*Hypotheses and Observations*).

So far the differences between the sexes as observed in adult forms. Attention must now be turned to the origin of sex itself in the individual organism. The historic beginning of sex will be discussed at a later stage; the present problem concerns the factors which determine whether any given organism will develop into a male or into a female. The question, in other words, is that usually known as the determination of sex.

§ 1. *The Period at which the Sex is Determined.*—Every organism, whether male or female, develops from a fertilised egg-cell, apart of course from the occurrence of asexual and parthenogenetic reproduction. This material, which in one case develops into a male, in another into a female, is, so far as our experience can go, always the same; and *when* the sex of the organism is absolutely decided, is a question to which no general answer can be given. In the higher animals (birds and mammals) it is possible at quite an early date in embryonic life to tell whether the young organism will turn into a male or a female, though in the very earliest stages it is impossible to determine whether the rudiment of the reproductive organs is going to become a testis or an ovary. But in lower vertebrates, such as frogs, the period of embryonic indifference is greatly prolonged; and it seems certain that a hatched tadpole, even after a tendency towards, say maleness, has actually arisen, may in certain conditions have this altered in the opposite direction. Among invertebrates, the sexual organs are often late in acquiring definite predominance in favour of either sex,—that is, the period of undecided indifference is, as one would expect, usually much longer.

The factors which are influential in determining sex are numerous, and come into play at different periods. The constitution of the mother, the nutrition of the ova, the constitution of the father, the state of the male element when

fertilisation occurs, the embryonic nutrition, and even the larval environment in some cases, these and yet other factors have all to be considered.

Some observations by Laulanié as to the embryonic organs are of interest in this connection. He distinguishes both in birds and mammals three stages in the individual development of the reproductive organs. These he calls (1) Germiparity, (2) Hermaphroditism, (3) Differentiated Unisexuality; and regards them as parallel to the stages of historic evolution. Even for the first stage, however, when the elements are still very primitive, he would not allow the accuracy of the terms neutrality or indifference. The elements in both sexes are almost similar, but yet their future fate has been decided.

Sutton has also emphasised his conviction, that in the individual development a state of embryonic hermaphroditism obtains, and maintains that one set of elements predominates over the other in the establishment of the normal unisexual state. Ploss and others take up a similar position in regard to an early hermaphrodite state. It can only be concluded, that the higher the organism is in the series the earlier is its sexual fate sealed; and that it is only in lower vertebrates, and among backboneless animals, that we can speak of prolonged neutrality of sex, or embryonic hermaphroditism.

§ 2. *Answers to the Question: What Determines Sex?*—To the question what determines whether an organism shall develop into a male or into a female, many and varied answers have been given. At the beginning of the last century, the theories of sex were estimated at as many as five hundred, and they have gone on increasing. It is evident that even an enumeration of these is not possible, nor is it indeed desirable. As in so many other cases, our ideas respecting the determination of sex have been looked at in three different ways. For the theologian, it was enough to say that "God made male and female." In the period of academic metaphysics, still so far from ended, it was natural to refer to "inherent properties of maleness and femaleness;" and it is still a popular "explanation" to invoke undefined "natural tendencies" to account for the production of males or females. This mode of treatment, it need not be said, is being abandoned by biologists. It is recognised that the problem is one for scientific analysis; thus the constitution, age, nutrition, and environment of the parents must be especially considered. These investigations, which are mainly restricted to observation and statistics, will be first noticed; the more experimental researches, and the general conclusions, will be discussed in the next chapter. Finally, a physiological

re-statement, in terms of protoplasmic metabolism, will be suggested.

§ 3. The theory that there are two kinds of ova, respectively destined to develop into males or females, is more than a mere begging of the question. The constitution of the ovum is undoubtedly a fact of primal importance, but we must also recognise the results of experiment, which show that later influences may also be determinative. The hypothesis of two kinds of ova was advanced, for example, by B. S. Schultze, but as the grounds for his views are not admitted as correct, only its existence need be noticed till more observations are forthcoming. Even if two kinds of ova were demonstrable, the question would remain what conditions determine the predominance of this or the other kind. What is the biological meaning of a family with seven daughters and one son? What is the biological meaning of Shufeldt's case of alternating sex in the five young birds which formed the brood of a sparrow-hawk? The oldest was male, the next female, and so on in regular alternation. ("Amer. Naturalist," xxxii., 1898, pp. 567-570, 1 fig.

§ 4. Numerous authors have attached great importance to the process of fertilisation as a determinant of the sex.

One of the most crude positions has been that of Canestrini, who ascribed the determination of sex to the number of sperms entering the ovum:—The more sperms, the greater the tendency to male offspring. It has, however, been shown by Fol, Pflüger, Hertwig, and others, that "polyspermy," or the entrance of more than one sperm, is extremely rare, is in fact generally impossible. In some of the cases where it is known to occur, it indicates a pathological condition of the egg-shell, and tends to produce abnormalities. Pflüger diluted the seminal fluid of male frogs, and found that no change resulted in the normal numerical proportion of the sexes. The case of drones, furthermore, where males are known to arise from unfertilised ova, is a familiar example, exactly counter to Canestrini's proposition, which may in fact be dismissed as wholly untenable.

§ 5. *Time of Fertilisation.*—With greater weight various authorities have insisted upon the time of fertilisation. Thus, according to Thury (1863), followed by Düsing (1883), an ovum fertilised soon after liberation tends to produce a female, while an older ovum will rather develop into a male. As a practical breeder Thury claimed to determine the sex of cattle upon this principle; Cornaz and Knight have both practically confirmed this; while Girou has pointed out that female flowers fertilised as soon as they were able to receive pollen tended to produce female offspring. Hertwig has also shown that the internal phenomena of fertilisation vary somewhat with the age of the ovum at the time. Hensen is inclined to accept the general accuracy of Thury's conclusion, but extends it to the male element as well. "A very favourable condition in both ovum and

sperm will probably lead to the formation of a female." "According to its condition, a sperm may either insufficiently corroborate the favourable state of the ovum, or constitutionally strengthen an ovum less satisfactorily conditioned." A side-light is thrown on this by Vernon's experiments on hybridising sea-urchins, which show that "the characteristics of the hybrid offspring depend directly on the relative degrees of maturity of the sexual products" ("Phil. Trans.," Series B, vol. cxc. (1898), pp. 465-529). The

Summary of Statistics bearing on Relative Number of Males and Females.

Observer.	No. of Births.	Locality.	Father older. Proportion of Males to 100 Females.	Father of equal age. Proportion of Males to 100 Females.	Father younger. Proportion of Males to 100 Females.	Average Proportion of Males to 100 Females.	Remarks.
Hofacker	1,996	Tübingen	117.8	92.0	90·6	107.5	..
Sadler	2,068	England	121.4	94.8	86.5	114.7	..
Göhlert	4,584	..	108.	93.3	82.6	105.3	..
Legoyt	52,311	Paris	104.49	102.14	97.5	102.97	..
Boulenger	6,006	Calais	109.98	107.92	101.63	107.9	..
Noirot	4,000	Dijon	99.7	..	116.0	103.5	..
Breslau	8,084	Zürich	103.9	103.1	117.6	106.6	..
Stieda	100,590	Alsace-Lorraine	105.03	..	108.39	106.27	Contradictory.
Berner	267,946	Sweden	104.61	106.23	107.45	106.0	Contradictory (see text).

same observer has shown that the degree of staleness of the ova and sperms of sea-urchins has an appreciable effect on the development ("P. Roy. Soc.," lxv. (1899), pp. 350-360).

§ 6. *Age of Parents.*—Hofacker (1823) and Sadler (1830) independently published a body of statistics, each including about 2,000 births, in favour of the generalisation that when the male parent is the older the offspring are preponderatingly male; while if the parents be of the same age, or

a fortiori if the male parent be the younger, female offspring appear in increasing majority. This conclusion, generally known as Hofacker's and Sadler's law, has received both confirmation and perplexing contradiction. It has been confirmed by Göhlert, Boulenger, Legoyt, and others, and by some breeders of stock and birds, but is denied by other practical authorities, and directly contradicted by the recent statistics of Stieda, from Alsace-Lorraine, and of Berner, from Scandinavia.

The above table (in its upper part taken mainly from Hensen, after Œsterlen) shows vividly how much the results of Stieda and Berner conflict with the law of Hofacker and Sadler. In regard to Berner's statistics, it ought to be further noted that the figures quoted refer to cases where the father or mother is only from 1 to 10 years the older. If the father be more than ten years older, the male majority is 103.54; if the mother be more than ten years older, the proportion is 104.10, again against Hofacker's and Sadler's conclusion. Compared with the above human statistics, Schlechter's results in regard to horses also militate against the alleged law.

In regard to plants, various naturalists have drawn attention to the influence of age upon sex. The following observations are quoted by Heyer:—In *Leontarus domestica*, according to Rumpf, the female plant may bear male blossoms before its proper female flowers. In *Morus nigra*, and in other cases, according to Miller, male flowers may be borne first, and afterwards fruit. Treviranus observed that the first flowers of beech, chestnut, and other trees are male. Clausen gives similar examples; and Hoffmann notes that in the horse-chestnut, and several other cases, male flowers appear first, and afterwards hermaphrodites or females.

Most of the results in regard to the influence of age are, however, extremely unsatisfactory and conflicting. This is evident from the above statistics. The law of Hofacker and Sadler cannot be regarded as in any sense established. In fact, as Hensen remarks, unless statistics are enormously large they prove very little. The number of other factors besides parental age which may operate in any case is evidently great, —health, nutrition, frequency of sexual intercourse, abstinence after the birth of a male, and the like, all reduce the feasibility of the statistical method. At present, at any rate, we are not justified in ascribing much importance to the relative age of the parent except as a secondary factor, influential doubtless in relation to nutrition.

§ 7. *Comparative Vigour.*—The best known, and probably still most influential, theory is that of "comparative vigour." As elaborated by Girou and others, this hypothesis connects the sex of the offspring with that of the more vigorous parent. It cannot be said, however, that facts bear out the case. Thus consumptive mothers produce a great excess of daughters, while Girou's theory would lead us to expect the opposite.

We require in fact to have "vigour" analysed out into its component factors, and in so doing we shall afterwards find not only facts but reasons in favour of the conclusion, in part included in the above theory, that highly nourished females tend to produce female offspring. That form of the hypothesis which refers the determination of sex to "genital superiority," or to "relative ardency," can hardly be seriously considered. In this connection it has been maintained that in "marriages of love," after a short betrothal, female offspring predominate; and a number of other interesting facts of a like nature are suggested. Some scepticism as to the practicability of such inductions is, however, inevitable.

§ 8. *Starkweather's Law of Sex.*—Closely allied to the theory of comparative vigour is that elaborately worked out by Starkweather, which is suggestive enough to deserve separate summary. He starts from a discussion of the alleged superiority of either sex. Few maintain that the sexes are essentially equal, still fewer that the females excel; the general bias of authority has been in favour of the males. From the earliest ages philosophers have contended that woman is but an undeveloped man; Darwin's theory of sexual selection presupposes a superiority and an entail in the male line; for Spencer, the development of woman is early arrested by procreative functions. In short, Darwin's man is as it were an evolved woman, and Spencer's woman an arrested man.

This notion of the superiority of males has formed the basis of many theories of sex. As a good illustration of this opinion, a few sentences may be quoted from Richarz:—"The sex is not a quality transmitted from the parents, but has its basis in the degree of organisation attained by the offspring. The male sex represents to a certain extent a higher grade of organisation or development in the embryo. This is attained when the reproductive efficiency of the mother is specially well developed, and the resulting male offspring more or less resembles the mother. But if the maternal reproductive power be weak, the ovum does not attain to maleness, and the resulting female offspring more or less resembles the father." Thus Hough thinks males are born when the maternal system is at its best; more females at periods of growth, reparation, or disease. Tiedman and others regard female offspring as arrested in the original state; while Velpau conversely regards females as degenerate from primitive maleness.

Reacting from such speculations as to superiority of either sex, Starkweather firmly maintains that "neither sex is physically the superior, but both are essentially equal in a physiological sense." This is true in the average, but yet in each pair a greater or less degree of superiority on one side or other must usually be conceded. Granting this, Starkweather states, as his chief conclusion, "that sex is determined by the superior parent, also that the superior parent produces the opposite sex." Referring the reader to the Ency. Brit. Article "SEX," for some critical notes, it is enough here to notice, that just like "comparative vigour," so "superiority" has little more than verbal simplicity to recommend it, since it lumps a great variety of factors under a common name. Yet, in justice to its author, we may admit that it is the algebraic sum of these which he aims at expressing.

§ 9. *Darwin's Position.*—Neither in regard to the origin of sex, nor its determination in individual cases, did Darwin see further than his contemporaries. He refers to the current theories of the influence of age, period of impregnation, and the like; and further contributes a great body of statistics on the numerical proportions of the sexes, and the supposed influence of polygamy. "There is reason," he says, "to suspect that in some cases man has by selection indirectly influenced his own sex-producing powers." He falls back upon the unanalysed "belief that the tendency to produce either sex would be inherited like almost every other peculiarity, for instance, that of producing twins." "In no case, as far as we can see, would an inherited tendency to produce both sexes in equal numbers, or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; . . . and therefore a tendency of this kind could not be gained through natural selection." "I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future." Any other hints that Darwin threw out, have been so well elaborated by Düsing's work on the advantageous self-regulation of the sex-proportions, that reference to the latter is more profitable.

§ 10. *Düsing on the Proportions of the Sexes, and the Regulation of these.*—In an important work, Düsing has

recently treated the whole subject with some synthetic result. He recognises that the fates or factors determining the sex are manifold, and operate at different periods. Much is determined by the condition of the reproductive elements—*i.e.*, by the constitution and habits of the parents; much depends also on the period of fertilisation; while again the nutrition of the embryo may be of moment. Düsing has collected a great body of facts, from both plants and animals, in favour of his conclusions; but the copious summary of his work, given in the article "SEX" already referred to, need not here be repeated, while some of his experimental results will be included in the next chapter.

Düsing's memoir is very important, however, for this special reason, that he analyses what may be termed the mechanism by which the proportion of the sexes is regulated. Instead of vaguely referring the whole matter to natural selection, he shows in detail how the numbers are in a sense self-regulating, how there is always produced a majority of the sex that is wanted. That is to say, if one sex be in the decided minority, or under conditions which come to the same thing, then a majority of that sex will be produced. If there be, for instance, a great majority of males, there is the greater likelihood of the ova being fertilised early, but that means a probable preponderance of female offspring, and thus the balance is restored. It would be rash to say that in every case he makes out his contention, but his general argument, that disturbances in the proportion of the sexes bring about their own compensation, is carefully and convincingly worked out.

§ 11. *Sex of Twins.*—It sometimes happens among many different classes of animals that from one ovum two organisms develop. We have then a case of "true" twins, as opposed to cases where multiple offspring do not arise from one ovum. Such "true" twins are said to occur not uncommonly in the human species, and are either most markedly similar to one another or strongly dissimilar.

From a very early date an exception to this rule has been known in regard to cattle, and applies to some other organisms as well. From the careful researches of Spiegelberg and others, it appears that in cattle (*a*) the twins may be both female and then both normal, or (*b*) that the sexes may be different and normal, or (*c*) that both may be males, in which case one always exhibits the peculiar abnormality known as a "free-martin." The internal organs are male, but the external accessory organs are female, and there are also rudimentary female ducts. No theory has yet explained the facts of this case.

It is now necessary, with Düsing for transition, to pass from the historical mode of treatment to something more constructive. Leaving mere hypotheses behind, as well as theories based on insufficient statistics, an induction from experimental evidence will be built up in the following chapter.

SUMMARY.

1. The epoch at which the sex is finally determined is variable in different animals, and diverse factors operate at successive epochs.

2. Theological and metaphysical theories of sex have preceded the scientific; observation and statistics have been resorted to before experiment; and over 500 theories in all have been set forth.

3-6. That there are two kinds of ova is still for the most part an assumption; that the entrance of more than one spermatozoon normally occurs, and is a determining factor, is erroneous. Thury's emphasis on the age of the ovum when fertilised is probably justified; while Hensen extends this notion to the male element as well. The age of the parents is probably only of secondary import, and the law of Hofacker and Sadler is not confirmed.

7, 8. Theories of "comparative vigour" and the like must be dismissed; while Starkweather's theory of the relative superiority of either sex, and of the influence of this on the sex of the offspring, requires further analysis.

9, 10. Darwin's position contains nothing novel, and has been superseded by Düsing's synthetic treatment and explanation of the self-regulating numerical proportion of the sexes.

11. From this point, after a note on the similar sex of "true" twins, we pass to the experimental data and constructive treatment.

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CHAPTER IV.

The Determination of Sex.

(Experiment and Rationale.)

§ 1. *Influence of Nutrition.*—Throughout nature the influence of food is undoubtedly one of the most important environmental factors. To Claude Bernard, indeed, the whole problem of evolution was very much a question of variations of nutrition. "L'evolution, c'est l'ensemble constant de ces alternatives de la nutrition; c'est la nutrition considerée dans sa réalité, embrassée d'un coup d'œil à travers le temps." It is fitting that we should begin our survey of the factors known to influence sex with the fundamental function of nutrition.

(*a*) *The Case of Tadpoles.*—Not a few investigators who have passed from statistics and hypothesis to experiment and induction, have found their material in tadpoles, where the sex seems to remain for a comparatively long period indeterminate. If we take the verdict of Yung, who has had much experience with these forms, tadpoles pass through a hermaphrodite stage, in common, according to other authorities, with most animals. During this phase external influences, and especially food, decide their fate as regards sex, though the hermaphroditism, as we shall afterwards see, sometimes persists in adult life. It is fair, however, to notice that Pflüger gives a somewhat different account of the actual facts, distinguishing among tadpoles three varieties—(*a*) distinct males, (*b*) distinct females, and (*c*) hermaphrodites. In the last, testes, or male organs, develop round primitive ovaries, and if the tadpoles are to become males the enclosed female organs are absorbed.

Adopting the view stated by Yung, we shall simply state the striking results of one series of observations. When the tadpoles were left to themselves, the percentage of females was rather in the majority. In three lots, the proportions of females to males were as follows:—54 : 46; 61 : 39; and 56 : 44. The average number of females was thus about 57 in the hundred.

In the first brood, by feeding one set with beef, Yung raised the percentage of females from 54 to 78; in the second, with fish, the percentage rose from 61 to 81; while in the third set, when the flesh of frogs was supplied, the percentage rose from 56 to 92. That is to say, in the last case the result of altered diet was that there were 92 females to 8 males. From the experience and carefulness of the observer, these striking results are entitled to great weight.

(*b*) *Case of Bees.*—The three kinds of inmates in a beehive are known to every one as queens, workers, and drones; or, as fertile females, imperfect females, and males. What are the factors determining the differences between these three forms? In the first place, it is believed that the eggs which give rise to drones are not fertilised, while those that develop into queens and workers have the normal history. But what fate rules the destiny of the two latter, determining whether a given ovum

The Queen (A), Worker (C), and Drone (B) of the Common Hive-Bee.

will develop into the possible mother of a new generation, or into the better-brained but non-fertile working female? It seems certain that the fate mainly lies in the quantity and quality of the food. Royal diet, and plenty of it, develops the reproductive organs of the future queens; sparser and plainer food retards the sexuality of the future workers, in which reproductive organs do not develop. Up to a certain point, the nurse bees can

determine the future destiny of their charge by changing the diet, and this in some cases is certainly done. If a larva on the way to become a worker receive by chance some crumbs from the royal superfluity, the reproductive function may develop, and what are called "fertile workers," to a certain degree above the average abortiveness, result; or, by direct intention, a worker grub may be reared into a queen bee.

The following table, after a recent analysis by A. von Planta, shows the differences of diet as far as solids are concerned. For queens 69.38 per cent., for drones 72.75 per cent., and for workers 71.63 per cent. is water.

SOLIDS.	Queens.	Drones. 1 to 4 days.	Drones. After 4 days.	Workers.
Nitrogenous	45.14	55.91	31.67	51.21
Fatty	13.55	11.90	4.74	6.84
Glucose	20.39	9.57	38.49	27.65
Ashes	4.06		2.02	

From the above, it is seen that the queen larvæ get a quantity of fatty material double that given to the workers. The drones at first receive a large percentage of nitrogenous material, but this soon falls below the share which workers and queens obtain. The fatty material, at first large, soon falls to about a third of that given to the queens. Hence the percentage of glucose, except at first, is so much larger than in the other two cases.

It is not necessary, however, to go into details to see the importance of the main point, that differences of nutrition, in great part at least, determine the all-important distinctions between the development and retardation of femaleness. Nor are there many facts more significant than this simple and well-known one, that within the first eight days of larval life, the addition of a little food will determine the striking structural and functional differences between worker and queen.

Eimer has drawn attention to the interesting correlation exhibited in the fact that a larva destined to become a worker, but converted into a queen, attains with the increased sexuality all the little structural and psychological differences which otherwise distinguish a queen. Regarding fertilisation as a sort of nutrition, he considers drones, workers, and queens as three terms of a series, and the same view is suggested by Rolph. Eimer recalls some interesting corroborations from humble bees. There the queen mother, awakened from her winter sleep by the spring sun, makes a nest, collects food, and lays her first

brood. These are not too abundantly supplied with nourishment, the queen having much upon her shoulders; they develop into small females, workers in a sense, but yet fertile, though only to the extent of producing drones. By-and-by a second brood of workers is born; these have the advantage of the existence of elder sisters, are more abundantly nourished, and develop into large females. Still, like the first brood, they produce drones, though occasionally females. Finally, with the advantage of two previous broods of small and large females, the future queens are born. The above facts not only afford an interesting corroboration of the influence of nutrition upon sexuality, but are of importance as suggesting the origin of the more highly specialised society of the hive bee.

(*c*) *Von Siebold's Experiments.*—With a somewhat different purpose than that at present pursued, Von Siebold made a series of careful observations on a species of wasp, *Nematus ventricosus*. These afford, as Rolph has noted, some valuable results in regard to the determination of sex. In this wasp, the fertilised ova, unlike those of hive bees, develop into males as well as females; while the unfertilised, or parthenogenetic eggs, may produce females in small percentage. From spring onwards, as warmth and food both increased, Von Siebold estimated the percentages of males and females in broods of larvæ reared from fertilised ova. The results of a series of observations may be condensed in a table :—

End of Larval Period (Pupation).	No. of Females to 100 Males.	No. of Females.	No. of Males.
15th June	14	19	136
July	77	86	66
July	269	579	215
August	340	..	..
End of August ..	500	..	..
September	100	..	..

As Rolph remarks, the results are not altogether satisfactory for the present purpose, "but this much is clear, that the percentage of females increases from spring to August, and then diminishes. We may conclude without scruple, that the production of females from fertilised ova increases with the temperature and with the food supply (*Assimilationsleistung*), and decreases as these diminish."

From the work of Rolph, which is full of a suggestiveness which the author unfortunately did not live to elaborate, we shall quote another paragraph summing up further experiments of Von Siebold :—

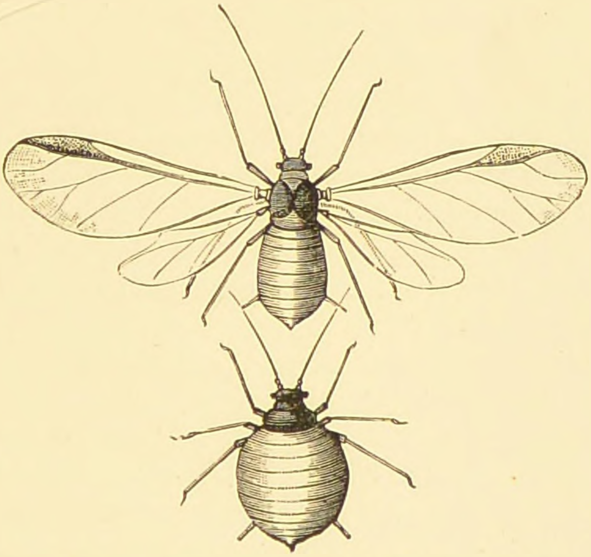
"Not less instructive," he says, "are the experiments with unfertilised ova (see Table).

"This table shows the same general result as before. The more abundant the metabolism (*Stoffwechsel*) and the nutrition, the greater

tendency to the production of females, which at the beginning and at the end are wholly absent. In the above series of experiments, they only appear when the metabolism and the nutrition were so abundant that the entire development of the young wasps only occupied eighteen or

No. of Experiment.	Duration of Embryonic and Larval State.	Sex.	
11	21 days	All Males.	
12	19 ,,	All Males.	
13	18 ,,	493 Males.	2 Females.
14	17 ,,	265 ,,	2 ,,
15	17 ,,	374 ,,	8 ,,
16	18 ,,	168 ,,	1 ,,
17	24 ,,	1 ,,	..

fewer days up to the period of pupation." The peculiarity in this last case, if the experiments were correct, is that in parthenogenesis, where the production of males is the normal condition, favourable environmental influences appear to introduce females.



Two Forms of a Common Plant-Louse or Aphis.—This figure may serve to illustrate three different things,—a winged male and a wingless female; a winged and a wingless parthenogenetic female; a winged sexual female, and an ordinary wingless parthenogenetic female.—From Kessler.

(*d*) *Case of Aphides.*—One of the most familiar illustrations of the influence of nutrition upon sex, is found in the history of the plant-lice or aphides, which is indeed full of other suggestions in regard to the whole theory of sex and reproduction. Details in regard to these plant-lice, which multiply so rapidly upon our rose-bushes, fruit-trees, and the like, differ

somewhat in the various species, but the general facts are recognised to be as follows. During the summer months, with favourable temperature and abundant food, the aphides produce parthenogenetically generation after generation of females. The advent of autumn, however, with its attendant cold and scarcity of food, brings about the birth of males, and the consequent recurrence of strictly sexual reproduction. In the artificial environment of a greenhouse, equivalent to a perpetual summer of warmth and abundant food, the parthenogenetic succession of females has been experimentally observed for four years,—it seems in fact to continue until lowering of the temperature and diminution of the food at once re-introduce males and sexual reproduction.

(*e*) *Butterflies and Moths.*—Still keeping to insects, we may note Mrs Treat's interesting experiment, that if caterpillars were shut up and starved before entering the chrysalis state the resultant butterflies or moths were males, while others of the same brood highly nourished came out females. Gentry too has shown for moths that innutritious or diseased food produced males, and suggests this as a partial explanation of the excess of male insects in autumn, although we suspect that temperature is in this instance probably more important.

It should be noted, however, that Paulton's experiments on the sexes of larvæ of *Smerinthus populi* give no support to the conclusion that the sex can be determined by external conditions during larval life. The larger female larvæ require more food, and when supplies are reduced they tend to starve first ("Trans. Entomol. Soc. London," 1893, pp. 451-6).

(*f*) *Crustaceans.*—In support of the same contention, Rolph has drawn attention to the following among other facts. One of the brine shrimps (*Artemia salina*) resembles not a few crustaceans in the local and periodic scarcity or absence of males, associated of course with parthenogenesis. At Marseilles, Rolph says, this artemia lives in especially favourable conditions, as its large size plainly indicates; there it produces only females. Where the conditions of existence are less prosperous, it produces males as well. "A certain maximum of abundance and optimum of vital conditions in parthenogenetic animals—daphnids and aphides, Apus, Branchipus, Artemia, and numerous other crustaceans—produce females; while less favourable conditions are associated with the production of males." In regard, however, to water-fleas

(daphnids), it is fair to notice that Rolph's conclusions do not quite consist with Weismann's, who, with unique experience in regard to these curious little animals, is disinclined to allow the direct influence of temperature and nutrition in the matter.

(*g*) In regard to Rotifers (*Hydatina*), Maupas maintains that temperature is the sex-determining factor, and that the sex of the offspring is determined two generations in advance! His experiments led him to conclude that when the ovum is being differentiated in the ovum, the temperature determines whether it shall develop into a male-producing or a female-producing individual. Nussbaum, on the other hand, disputes the conclusiveness of this result, and maintains that nutrition is the determining factor: females of *Hydatina* which have been insufficiently fed during early life afterwards lay only male eggs, while well-nourished forms produce female eggs.

(*h*) *Mammals.*—When we pass to higher animals, the difficulties of proving the influence of nutrition upon sex are much greater. Yet there are decisive observations which go to increase the cumulative evidence. Thus an important experiment was long ago made by Girou, who divided a flock of three hundred ewes into equal parts, of which the one-half were extremely well fed and served by two young rams, while the others were served by two mature rams and kept poorly fed. The proportion of ewe lambs in the two cases was respectively sixty and forty per cent. In spite of the combination of two factors, the experiment is certainly a cogent one. Düsing brings forward further evidence in favour of the same conclusion, noting, for instance, that it is usually the heavier ewes which bring forth ewe lambs. He emphasises the fact that the females having a more serious reproductive sacrifice, are more dependent on variations of nutrition than males. Even in birds, as Stolzmann points out, there is a much greater flow of blood to the ovary than to the testes,—the demands are greater, and the consequences therefore more serious if these are not fulfilled.

(*i*) In the human species, lastly, the influence of nutrition, though hard to estimate, is more than hinted at. Ploss may be mentioned as an authority who has emphasised this factor in homo. Statistics seem to show, that after an epidemic or a war the male births are in a greater majority than is usually the case. Düsing also points out that females with small

placenta and little menstruation bear more boys, and contends that the number of males varies with the harvests and prices. In towns, and in prosperous families, there seem to be more females, while males are more numerous in the country and among the poor.

Schenk has (1898) re-enunciated the view that nutrition is the chief determining factor in deciding the sex of offspring But his evidence is quite insufficient; indeed, when it is critically examined it is seen to consist of three or four cases.

(*j*) *Determination of Sex in Plants.*—It is at present extremely difficult to come to any very satisfactory conclusion in regard to the influence of nutrition upon the sex of plants. The whole subject, as far as its literature is concerned, has been recently discussed by Heyer, but his survey is by no means a sanguine one. His conclusions, in fact, seem to land him in a scepticism as to all modification of the organism by environmental influences, which we should of course be far from sharing. It must be admitted that the experiments of Girou (1823), Haberlandt (1869), and others, yielded no certain result; while the conclusions of some others are conflicting enough to justify not indeed Heyer's despair, but his present caution. Still a few investigations, especially those of Meehan (1878), which are essentially corroborated by Düsing (1883), go to show, for some cases, that abundant moisture and nourishment do tend to produce females. Some of Meehan's points are extremely instructive. Thus old branches of conifers, overgrown and shaded by younger ones, produce only male inflorescence. In the American *Corylus rostrata*, and in many other instances, he is convinced that in early stages the sex of a flower-bud is undetermined, and that its determination as a male or female flower is mainly the result of the nutritive conditions ("Proc. Acad. Nat. Sci. Philadelphia," 1899, pp. 84-86). Various botanists, quoted by Heyer, confirm one another in the observation that prothallia of ferns grown in unfavourable nutritive conditions produce only antheridia (male organs), and no archegonia (female organs).

The botanical evidence, though by no means strong, corroborates the general result that good nourishment produces a preponderance of females. The contrast of the sexes in some of our common diœcious plants is here very instructive. Taking for instance the dog-mercury (*Mercurialis perennis*) of

any shady dell, or the day lychnis (*L. diurna*), hardly less abundant on the sunnier slopes, experiments are still certainly wanting with regard to given plants, as to what circumstances originally determined their sexual differences; but the fact of superior constitutional vegetativeness in the females is here so peculiarly obvious, that it can hardly fail to arouse a strong impression that more or less advantageously nutritive conditions, whether of the embryo or of the seedling, are sufficient to account for the differences of sex.

§ 2. *Influence of Temperature.*—In this connection not a few writers have referred to an observation by Knight, which, from its comparatively ancient date, perhaps deserves to be recorded in his own words, if only to show the necessity of caution in such matters. A water-melon was grown in a heated glass-house, where the temperature sometimes rose on warm days to 110° Fahr. "The plant grew with equal health and luxuriance, and afforded a most abundant blossom; but all its flowers were male. This result did not in any degree surprise me, for I had many years previously succeeded, by long continued very low temperature, in making cucumber plants produce female flowers only; and I entertain but little doubt that the same fruit stalks might be made, in this and the preceding species, to support either male or female flowers in obedience to external causes."

This experiment was obviously more sanguine than satisfactory. Heyer justly points out that of the water-melon only a single plant was taken. Furthermore, he says, the water-melon in nature usually bears only female flowers on the apices of the older twigs, and may bear only a minimum number of these. Knight's observations on cucumbers are also open to serious objections, and were too scanty to prove anything.

Meehan finds that the male plants of hazel grow more actively in heat than the female; and Ascherson has made the interesting observation that the water-soldier (*Stratiotes aloides*) bears only female flowers north of 52° lat., and from 50° southwards only male ones. On the other hand, Molliard maintains ("Comptes Rendus," cxxvii., 1898, pp. 669-671) that in the case of dog's mercury (*Mercurialis annua*) a high temperature favours the production of female individuals, but whether the heat simply promotes especially the development of the female seeds, or has some direct effect on the nature of the seed, is left undetermined. The same experimenter maintains in regard

to the hop that the sex is not absolutely determined in the seed, and that a transformation may be observed from male to female inflorescences under conditions that are very unfavourable to the development of the vegetative organs, *e.g.*, feeble illumination.

In the human species, Düsing and others have noted that more males are born during the colder months; and Schlechter has reached the same results from observations upon horses. The temperature of the time, not of birth but of sex determination, is however more important; nor must it be forgotten that temperature may have many indirect and subtle influences.

§ 3. *Summary of Factors.*—If we now sum up the case, it must first be recognised that a number of factors co-operate in the determination of sex; but that the most important of these may be more and more resolved into plus or minus nutrition, operating upon parent, sex elements, embryo, and in some cases larvæ.

(*a*) Starting with the parent organisms themselves, we find this general conclusion most probable,—that adverse circumstances, especially of nutrition, but also including age and the like, tend to the production of males, the reverse conditions favouring females.

(*b*) As to the reproductive elements, a highly nourished ovum, compared with one less favourably conditioned, in every probability will tend to a female rather than to a male development. Fertilisation, when the ovum is fresh and vigorous, before waste has begun to set in, will corroborate the same tendency.

(*c*) Then if we accept Sutton's opinion as to a transitory hermaphrodite period in most animals, from which the transition to unisexuality is effected by the hypertrophy of the female side or preponderance of the male in respective cases, the vast importance of early environmental influences must be allowed. The longer the period of sexual indifference (though this term be an objectionable one) continues, the more important must be those outside factors, whether directly operative or indirectly through the parent. Here again, then, favourable conditions of nutrition, temperature, and the like, tend towards the production of females, the reverse increase the probability of male preponderance.

The general conclusion, then, more or less clearly grasped by numerous investigators, is that favourable nutritive con-

ditions tend to produce females, and unfavourable conditions males.

§ 4. Let us express this, however, in more precise language. Such conditions as deficient or abnormal food, high temperature, deficient light, moisture, and the like, are such as tend to induce a preponderance of waste over repair,—a *relatively katabolic* habit of body,—and these conditions tend to result in the production of *males*. Similarly, the opposed set of factors, such as abundant and rich nutrition, abundant light and moisture, favour constructive processes, *i.e.*, make for a *relatively anabolic* habit, and these conditions tend to result in the production of *females*. With some element of uncertainty, we may also include the influence of the age and physiological prime of either sex, and of the period of fertilisation. But the general conclusion is tolerably secure,—that in the determination of sex, influences inducing a relative predominance of katabolism tend to result in production of males, as those favouring a relative predominance of anabolism similarly increase the probability of females.

§ 5. This is not all, however; the above conclusion is indeed valuable, but it acquires a deeper significance when we take it in connection with the result of a previous chapter. There it was seen, as the conclusion of an independent induction, that the males were forms of smaller size, more active habit, higher temperature, shorter life, &c.; and that the females were the larger, more passive, vegetative, and conservative forms. Theories of "inherent" maleness or femaleness were rejected, since practically merely verbal; more accurately, however, they have been interpreted and replaced by a more material conception, which finds the bias of the whole life, the resultant of its total activities, to be a predominance of the protoplasmic processes either on the side of disruption or construction. This conclusion has still to receive cumulative proof, but one large piece of evidence is now forthcoming, that, namely, of the present chapter. If influences favouring katabolism make for the production of males, and if anabolic conditions favour females, then we are strengthened in our previous conclusion, that the male is the outcome of relatively predominant katabolism, and the female of relatively predominant anabolism.

§ 6. *Weismann's Theory of Heredity.*—In thinking of the environment as a factor determining the sex, it is impossible to ignore that such facts as we have noted above have some

bearing upon the problem of heredity. Much of the recent progress in the elucidation of the facts of inheritance has been due to Weismann, who, in his theory of the continuity of the germ-plasm, has restated the very important and fundamental conception of a continuity between the reproductive elements of one generation and those of the next. To this restatement we shall afterwards have to refer; it is with another position, not peculiar to, but emphasised by the same authority, that we have here to do, viz., with his denial of the inheritance of individually acquired characters. Any new character exhibited by an organism may arise in one of two ways, which it is easy enough to distinguish theoretically;—it may be an outcrop of some property inherent in the fertilised egg-cell, that is, it may have a constitutional or germinal origin; but, on the other hand, it may be impressed upon the individual organism by the environment, or acquired in the course of its functioning, that is, it may have a functional or environmental origin. But all such functional and environmental modifications are, according to Weismann, restricted to the individual organism; they are not transmissible.

In this denial of the transmission of dints from without, and of acquired habits other than constitutional, Weismann expresses a scientific scepticism, based on the one hand on the absence of data demonstrating what we may still call the current belief, and on the other hand on the improbability of modifications reacting from the "body" on the reproductive cells in such a specific and representative way that the offspring inherit the modifications even in the slightest degree. If such a reaction do not occur, Weismann's position is secure; and though in a system saturated with alcohol, or transferred to a new climate, the reproductive cells may vary *along with* the body, no modification of nerve or muscle can, as such, be transmitted in inheritance.

The relative scarcity of experimental data, the divergence of opinion as to the pathological evidence, and the difficulty of applying our logical or anatomical distinctions to the intricate facts of nature, make decisive statements impossible, but it may be said that no clear case of the transmission of an acquired modification has as yet been forthcoming.

Weismann's position—slightly modified to meet criticism—must not be held to imply that the germ-cells lead a "charmed life," insulated, as it were, from the general life of the body.

That would indeed be a "physiological miracle," and it may be safely said that no one believes in any such apartness. At the same time, it may be useful to recall the facts of this chapter in order to avoid exaggeration of the degree to which the germ-cells are uninfluenced by modifications in the body. For in such a case as Yung's tadpoles, influence of nutrition saturated through the organism and did affect the reproductive elements, not indeed to the degree of altering any structural feature of the species, but yet to the extent of altering the natural numerical proportions of the sexes. But it must be clearly understood that this does not really touch the precise question of the inheritance of acquired characters.

SUMMARY.

1. Nutrition is one of the most important factors in determining sex. In illustration, note (*a*) the experiments of Yung, which raised the percentage of females from 56 to 92 by good feeding; (*b*) the case of bees, where the differences between queen and worker well illustrate the enormous results of a slight nutritive advantage; also the case of humble-bees, with three successive broods increasing in nutritive prosperity and in femaleness; (*c*) Von Siebold's experiments with a wasp, which showed most females in favourable conditions; (*d*) Aphides, in prosperity of summer, yield a succession of parthenogenetic females, in cold and scarcity of autumn males return; (*e*) among starved caterpillars of moths and butterflies more males survive; (*f*) Rolph's observations on crustaceans; (*g*) experiments on Rotifers; (*h*) also the facts noted by Girou, Düsing, and others, on the influence of good nourishment of mammalian mothers in favouring female offspring; (*i*) the hints of the same results in the human species; (*j*) various observations in regard to plants favouring the same general conclusion.

2. As to the influence of temperature, favourable conditions again tend to femaleness of offspring, extremes to males.

3. These factors are now added up—(*a*) the nutrition, age, &c., of parents; (*b*) the condition of the sex elements; (*c*) the environment of embryo.

4. The generalisation is thus reached—anabolic conditions favour preponderance of females, katabolic conditions tend to produce males.

5. But females have been already seen to be relatively more anabolic, and females relatively more katabolic. This view of sex is therefore confirmed.

6. The determination of sex illustrates an outside influence penetrating to the reproductive cells, but this does not touch the precise question as to the inheritance of acquired characters.

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BOOK II.

ANALYSIS OF SEX—ORGANS, TISSUES, CELLS.

CHAPTER V.

SEXUAL ORGANS AND TISSUES.

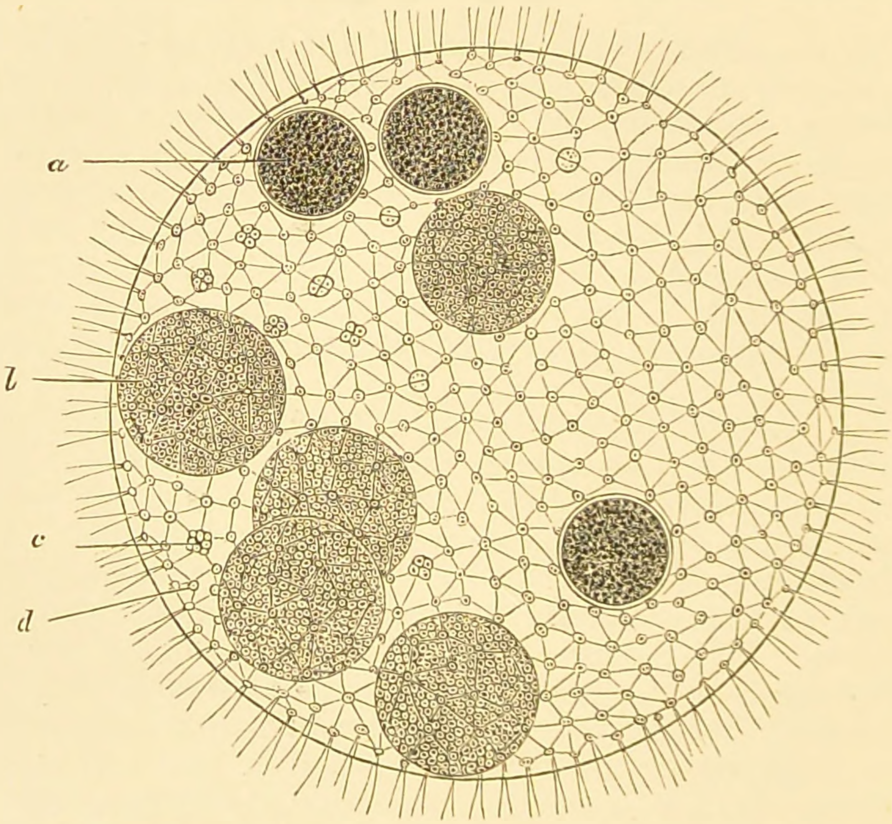
IT is the object of this portion of the book to continue the analysis of sexual characters, but now in a deeper way, reviewing successively the organs, tissues, and cells concerned in sexual reproduction. The essential and auxiliary organs of the two sexes, the frequent combination of these in hermaphrodite plants and animals, the sex-cells both male and female, will be discussed in order. This survey will be for the most part structural or morphological; the physiological aspects of sexual union and of fertilisation will be discussed at a later stage.

§ 1. *Essential Sexual Organs of Animals.*—It is now a well-established fact that among the ciliated infusorians, which swarm especially in stagnant waters, a process occurs which cannot but be described as in part sexual reproduction. Two individuals, to all appearance alike, become temporarily associated, exchange portions of their (micro-) nuclei, and then separate. This process of fertilisation is essential to the continued vigour of the species, and will be afterwards described at length. Such a very simple form of sexual union differs from what occurs in higher animals in two conspicuous respects,—(*a*) the organisms are apparently quite similar in form and structure; (*b*) they are unicellular, and thus there is no distinction between "body" and reproductive cells. What is fertilised by the mutual exchange in those infusorians is, roughly speaking, the entire animal, for the whole is but a corpuscle of living matter.

Among the Protozoa, however, loose colonies of cells occur, which bridge the gulf between unicellular and multicellular animals. In these we find the first indications of the afterwards conspicuous difference between "body" and reproductive cells. From these loose colonies, certain of the units are set adrift, and meeting with others more or less like

themselves, fuse to form a double cell, virtually a fertilised ovum, from which by continuous division a fresh colony is then developed. In these transition forms there are thus reproductive cells of slight distinctness, but as yet obviously no sexual organs.

When we pass to the sponges, we find colonies consisting of myriads of cells, among which there is a considerable division of labour. An outer layer (or ectoderm) usually consisting of much subordinated cells, an inner layer (or endoderm) of pre-



Volvox, a colony of cells, with some set apart for reproduction, after Klein.

dominantly active and well-nourished cells, a middle laye of heterogeneous constituents, can be distinguished. Every average infusorian is as good as its neighbours, so far as reproduction of new individuals by division is concerned; in the colonial Protozoa, the units that are set adrift are very little different from their fellows that remain behind; but this ceases to be true when we pass to colonies where considerable division of labour has been established. It is certainly true that even a tiny fragment of sponge, cut off from the larger mass, may,

if it contain sufficient samples of the body, and if the conditions be favourable, reproduce a new individual. Cultivators of bath sponges sometimes take advantage of this fact. But the sponge starts its new colonies for itself usually in quite a different way, namely, by the process of sexual reproduction. Among the cells of the middle stratum of the sponge body certain well-nourished passive cells appear. These are the ova, at first very like, but eventually well marked from the other constituent units of the layer. Besides these there are other cells, either in the same sponge or in another, which exhibit very different characters. Instead of growing large and rich in reserve material like the egg-cells or ova, they divide repeatedly into clusters of infinitesimal cells, and form in so doing the male elements or spermatozoa. The male and female cells meet one another, they form a fertilised ovum; the result is continued division of the latter till a new sponge is built up. Here then there are special reproductive cells, quite distinct from those of the "body"; and here, furthermore, these reproductive cells are markedly contrasted as male and female elements. As yet, however, there are no sexual *organs*.

Passing to the next class, the stinging animals or cœlenterates, we find in one of the simplest and most familiar of these, the common fresh-water hydra, a good illustration of primitive sexual organs. As in sponges, a cut-off fragment of the body, if sufficient samples of the different component cells are included, is able to reconstitute the whole. But no one body-cell has of course any such power; this is possible for the fertilised ovum alone. Now this ovum occurs, not anywhere within a given layer as in sponges, but always near one spot on the body. Towards the base of the tube a protuberance of outer layer cells is developed. This forms a rudimentary *ovary*, or female organ. It has this peculiarity, not however unique, that while the organ consists of not a few cells, only one of these becomes an ovum. A similar protrusion, or more than one, often at the same time and on the same animal, may be recognised further up the tube, nearer the tentacles of the hydra. Smaller than the ovary, each protuberance consists of numerous small cells, most of which, multiplying by division, form male elements or spermatozoa. We have here the simplest possible male organ or *testis*.

More elaborate organs occur in the other cœlenterates, complicated however by two interesting facts, which will be

afterwards discussed. (*a*) Many of the cœlenterates are well known to form elaborate colonies,—zoophytes, Portuguese men-of-war, and the like. In these, division of labour frequently goes further than the setting apart of special organs. Entire individuals become reproductive "persons" (as they are technically called), in contrast to the nutritive persons of the colony. (*b*) In some of those reproductive individuals, a curious phenomenon, known as migration of cells, has been observed by Weismann and others. The reproductive cells, arising in various parts of the body, have been shown to migrate in some cases to another part, where they find final lodgment in more or less definite organs. This occurrence is intimately associated with "alternation of generations," and will be afterwards discussed under that heading.

It is far from the purpose of the present work to describe the details respecting the ovaries and testes, as they occur in the various classes of animals. It is enough for our purpose to have emphasised the fact of their gradual differentiation, and to note that they are almost always developed in association with the middle layer of the body, and usually occupy a posterior position on the wall of the body-cavity. The details will be found in any standard work on comparative anatomy, very conveniently for example in Professor Jeffrey Bell's "Comparative Anatomy and Physiology," London, 1885.

§ 2. *Associated Ducts.*—It is only in a few animals, like hydra and its allies, that the ovaries and testes are external organs, which have simply to burst to liberate their contents. They are of course usually internal, and thus arises the necessity of some means of communication with the outside world. In the simplest cases, the male elements find their way out to the surrounding medium without any specialised mode of exit. They there meet, by chance combined with physical attraction at short range, with the ova, which in the simplest cases again have found their way out in an equally primitive fashion. Thus in the enigmatical parasitic Mesozoa (Orthonectids, &c.), liberation of the germs may occur by perforation or by rupture of the excessively simple bodies. In some of the marine worms (*e.g. Polygordius*), the liberation of the ova at least is accompanied by the fatal rupture of the mother organism, a vivid instance of reproductive sacrifice. Even in some of the common nereids, the same uneconomical mode of liberation by rupture appears to occur. The forcible rupture may be referred to pressure of the relatively large mass of growing cells which the ovaries often present.

As high up as back-boned animals, the absence of ducts may be traced. Thus among the sea-squirts or tunicates, the reproductive organs are frequently ductless, and the same thing is true of some fishes. The sex-cells burst into the body-cavity, and thence find their way to the exterior by

apertures. In most cases, where ducts are absent, fertilisation of the ova is external, but this is not necessarily so. In sponges, for instance, fertilisation is almost always internal. Male elements are washed in by the water-currents, find their way to the ova, and fertilise them *in situ*. Almost without exception, embryo-sponges, not ova, make their way to the exterior. In the higher animals, where definite ducts are present, alike for the inward passage of spermatozoa and the exit of ova or embryos, it ought further to be noticed that the ovaries can hardly ever be said to be in direct connection with their ducts. The ova usually burst from the ovary into the body-cavity, whence they are more or less immediately caught up by, or forced into the canals, by which they pass outwards. With the testes it is different, for if ducts be present, they are in direct connection with the organs.

It is enough to state that in the great majority of cases ducts are associated with the essential organs. Those of the male serve for the exit of the spermatozoa, and may be terminally modified as intromittent organs. Those of the females serve either solely for the emission of unfertilised eggs, or for the reception of spermatozoa, and the subsequent exit of fertilised ova or growing embryos. In some worm-types, and in all vertebrates, from amphibians onwards, the reproductive ducts are also in various degrees associated with excretory functions. For an account of the origin of the ducts in higher animals, the reader must be referred to the embryological text-books of Balfour, Hertwig, Haddon, Marshall, and others. Similarly for such modifications as that of the female duct into oviduct and uterus, reference must be made to the larger anatomical works of Gegenbaur and Wiedersheim, or for a briefer account to Parker's translation and edition of Wiedersheim's smaller text-book, and to Professor Jeffrey Bell's work already mentioned.

§ 3. *Yolk-Glands.*—As we shall afterwards see, the ovum is often furnished with a large quantity of nutrient material. This serves as the food-capital for the growing embryo or young larva. It is obtained in various ways,—from the vascular fluid, from the sacrifice of adjacent cells, or from special organs known as yolk-glands or vitellaria. The yolk-glands, as they occur for instance in some of the lower worms (turbellarians, flukes, tapeworms), are of some general interest. They represent, as Graff has shown, a degenerate portion of the ovary, in which the cells have become even more highly anabolic than ova. "The origin of the yolk-gland," Gegenbaur says, "is probably to be found in the division of labour of a primitively very large ovary." In more technical language, yolk-glands are hypertrophied or hyper-anabolic portions of the ovary. Apart from this nutritive capital, the egg is often equipped with envelopes or shells of some sort, which may be furnished by special organs, or by the sacrifice of surrounding cells, or by the walls of the ducts as the eggs pass out.

§ 4. *Organs Auxiliary to Impregnation.*—In most animals

in which internal fertilisation of the ova occurs, there are in both sexes special structures auxiliary to the function of impregnation. Thus the end of the male canal is commonly modified into an intromittent tube or penis, through which the male elements flow into the female duct. In the crustaceans some of the external appendages are often modified, as in the crayfish, to serve this purpose, and the same is the case with minute structures on the posterior abdomen of many insects. Sometimes, as in the snail (*Helix*), which may be taken as an extreme type of reproductive specialisation, separate organs are present, in which the spermatozoa are compacted into masses or packets, known as spermatophores. In most cuttle-fishes, these pass from the male ducts to one of the "arms," which thus laden is occasionally set free bodily into the mantle-cavity of the female, where it was of old mistaken for a worm, and called *Hectocotylus*. So in some spiders, the palps near the mouth receive the male elements, and transfer them to the female. Special storing receptacles and secreting glands are also very frequently in association with the male ducts, and there is a long list of curious modifications utilised in the process of copulation. Thus, male frogs have swollen first fingers, and gristly fishes have "claspers," which are modified parts of the hind limbs, and are inserted into the cloaca of the female. The common snails eject a limy dart (*spiculum amoris*), which appears to be a preliminary excitant to copulation.

So too, in the female sex, the terminations of the duct may be modified for reception of the male intromittent organ, and special receptacles may be present for storing the spermatozoa. Where a single fertilisation occurs, as in the queen bee, previous to a long-continued egg-laying period, the importance of a storing organ is obvious. As the female is usually more or less passive during copulation, the adaptations for this purpose are less numerous than in the males. It is interesting to notice, that, among amphibians, where the male often takes upon himself distinctly maternal duties, one case is known where the female seems more active than the male during copulation.

§ 5. *Egg-Laying Organs.*—Cases where the ova simply pass out into the water, or on to the land, are of course associated with the absence of any special organs. In a great many animals, however, more care is taken, and auxiliary structures are present. One of the simplest of useful developments is exhibited by glands, the viscid secretion of which moors the

ova, and keeps them from being set wholly adrift. In insects, where it is specially important that the eggs should be well concealed, or buried in conveniently nutritive material, hints of the ancestral abdominal appendages remain as "ovipositors." Throughout the series a great variety of structures occur in this connection.

§ 6. *Brooding and Young-Feeding Organs.* — From very lowly animals onwards, structures are present which are utilised in the protection of the young in their helpless stages. The reproductive buds of some cœlenterates become true nurseries; in one at least of the marine worms (*Spirorbis spirillum*), a tentacle serves as a brood pouch; various adaptations, such as tents of spines, or cavities in the skin, are utilised in echinoderms. The young shelter under the hard cuticle, or among the appendages of crustaceans, and in the gills of some bivalves. The pockets of not a few fishes, the cavities on the back of the Surinam toad, the pouches of marsupials, are only a few instances amid a crowd. Sometimes, especially in fishes and amphibians,—*e.g.*, the sea-horse, with its breast-pouch, and *Rhinoderma darwinii*, with its enlarged croaking sacs,—it is the male which undertakes the brooding office.

When the young are born alive, the internal female ducts become developed in this connection to form uteri. The ovary appears to serve as a womb in the genus *Girardinus* among fishes, but it is usually the median portion of the female duct which has this function. In placental mammals, where the young are born at an advanced stage, and where the maternal sacrifice is at its maximum, the uterine adaptations become more important and complex. The organs of lactation will be afterwards discussed.

In illustration of the strange inter-relations between different forms, we may refer to the fresh-water mussels. The larvæ or Glochidia are sheltered and nourished in the outer gill-plates of the female, and are liberated when fishes come near. To the skin of these the larvæ fix themselves, become temporarily parasitic, and undergo a metamorphosis, after which they fall off. Without the presence of fishes the life-history cannot be completed. On the other hand, the young stages of the fresh-water fish known as the bitterling (*Rhodeus amarus*) find temporary shelter in the gills of the mussels.

SUMMARY.

1. The gradual differentiation of essential sexual organs in animals,—isolated cells, aggregated tissues, definite organs.

2. Associated male and female ducts for the liberation of male-elements, fertilisation, exit of ova, or birth of embryos.

3. Yolk-glands, &c., for nourishment and equipment of the ova. Vitellaria have been interpreted as degenerate ovaries.

4. Illustrations of organs auxiliary to impregnation. In the male,—penis, storing sacs, spermatophore-making organs, "claspers." Curiosities, such as the hectocotylus of cuttle-fishes, and the Cupid's dart of snails. Adaptations in the female are less frequent, but storing receptacles for the male-elements are common.

5. Egg-laying organs:—frequency of ovipositors.

6. Brood-pouches and the like are widely present in most classes of animals.

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CHAPTER VI.

HERMAPHRODITISM.

§ 1. When an organism combines within itself the production of both male and female elements, it is said to be bisexual or hermaphrodite. This is the case with many of the lower animals,—such, for instance, as earthworms and snails. It is not desirable to extend the term, as is sometimes done, to cases like ciliated infusorians, where sex itself is only incipient. In flowering plants, the stamens and carpels, which produce microspores and macrospores respectively, are often, though inaccurately, called the male and female organs, and when both are present in the same flower the term hermaphrodite is often used. But the flowering plant is a sporophyte with only a vestige of the sexual generation left, and the term hermaphrodite should be kept for cases like the prothallus of a fern—a sexual generation with male and female organs on the same small expansion. While the general definition of hermaphroditism, as the union of the two sexes in one organism, is plain enough, the union is exhibited in a great variety of ways and degrees. Of these it is necessary first to take account.

§ 2. *Embryonic Hermaphroditism.*—Some animals are hermaphrodite in their young stages, but unisexual in adult life. Allusion has already been made to the case of tadpoles, where the potential bisexuality occasionally lingers into adult life. According to some, most higher animals pass through a stage of embryonic hermaphroditism, but decisive proof of this is wanting.

The research of Laulanié may now be referred to at greater length. As the result of observations on the development of the reproductive organs in the higher vertebrates, and especially in birds, he seeks to establish a strict parallelism between the individual, and what he believes to have been the racial history. In the chick, he distinguishes three main stages in the development—(1) germiparity, (2) hermaphroditism, (3) differentiated unisexuality. These he regards as recapitulating the great steps of the historic evolution. (1.) For the first period of "germiparity,"—from the

fourth to the sixth day,—the designation, sexual neutrality, or indifference, is inappropriate, since the "cortical ovules" of the germinal epithelium have from the first the precise morphological significance of female elements or ova. In the female, they proceed by multiplication to form the ovary; in the male, they degenerate. (2.) The period of hermaphroditism begins with the seventh day. In the male, the male ovules, from which the sperms are afterwards developed, appear in the central tissue; but at the same time cortical or female ovules may be seen persisting. Similarly, in the developing ovary of the female, the central or medullary portion, strictly separated by a partition of connective tissue from the egg-forming layer, contains a large number of medullary or male ovules. (3.) This hermaphroditism is of short duration. The cortical or female ovules disappear from the testes by the eighth or ninth day; and the medullary or male ovules have by the tenth day disappeared from the ovary. In regard to mammals, Laulanié affirms, allowing some peculiarities, that the same three stages of germiparity, hermaphroditism, and unisexuality occur.

Ploss has already been referred to as another investigator who maintains the existence of embryonic hermaphroditism. Such also is the view held by Professor Sutton, who concludes that both sets of organs are equally developed up to a definite period, and emphasises the consequent necessity for the hypertrophy of one sexual rudiment over the other.

§ 3. *Casual or Abnormal Hermaphroditism.*—In many species which are normally unisexual, a casual hermaphrodite form occasionally presents itself. The embryonic equilibrium or bisexuality—one of the two must in a variable degree exist—is retained as an abnormality into adult life Even as far up in the organic series as birds and mammals, such casual and yet true hermaphrodites occur. In most cases at least the result is sterility. Among amphibians, which abound in reproductive peculiarities, hermaphroditism exceptionally occurs, and in some species of toad it seems to be constant. The common frog, so much dissected in our laboratories, has supplied several good illustrations. Thus Marshall notes that the testes may be associated with genuine ova, or an ovary may occur on one side, and a testis with an anterior ovarian portion upon the other. Bourne gives a case of a frog with the ovary well developed on the right side, and opposite this an ovary anteriorly replaced by testis. One of the toads (*Pelobates fuscus*) seems to be frequently hermaphrodite, the male being furnished with a rudimentary ovary in front of the testes. A similar hermaphroditism is not at all infrequent in cod, herring, mackerel, and many other fishes. Sometimes a fish is male on one side, female on the other, or male anteriorly and female posteriorly. Sir J. Y. Simpson, in a learned article on the subject, has distinguished cases of true hermaphroditism, according to the position of the organs, into lateral, transverse, and vertical or double. Among invertebrates the same has been occasionally observed, especially among butterflies where striking differences in the colouring of the wings on the two sides have in some cases been found to correspond to an internal co-existence of ovary and testis. The same has been observed in a lobster, and is probably commoner than the recorded cases warrant one in asserting. As low down as cœlenterates, casual hermaphroditism may occur, as F. E. Schulze showed in one of the medusoids.

§ 4. *Partial Hermaphroditism.*—An organism may be said to be truly hermaphrodite when both male and female organs are present, or when,

without there being separate organs, both male and female elements are produced. It is then both anatomically and physiologically hermaphrodite, and of this, as we shall see, there are abundant illustrations among lower animals. Snail, earthworm, and leech are examples of this hermaphroditism, in varying degrees of intimacy.

But, as we have just noticed, a species normally unisexual may occasionally exhibit hermaphrodite individuals. In these only one of the double essential organs may be functional, or both may be sterile. Whether physiologically or not, such animals are anatomically hermaphrodite. Both kinds of essential organs are at least present.

To those must now be added a further series of cases to which the term partial hermaphroditism seems most applicable. Only one kind of sexual organ, ovary or testis, is developed; but while one sex preponderates, there are more or less emphatic hints of the other. As the reproductive organs are to be regarded as the most important, but not by any means the sole expression of the fundamental sex-differences, it is impossible to separate partial hermaphroditism by any hard and fast line from the above, and from the next set of cases (paragraphs 3 and 5). Almost all cases of partial hermaphroditism occur as exceptions, though a few are constant.

In the higher animals, partial hermaphroditism is usually expressed in the nature of the reproductive ducts. In this connection the structural resemblance of the male and female organs must be once more emphasised. Even the Greeks had their vague and fanciful theories of what we now call the homology of the reproductive organs and ducts in the two sexes. Through the labours of the anatomists of Cuvier's school, such as his fellow-worker Geoffroy St Hilaire, and yet more through more recent embryological discoveries, there is now both clearness and certainty as to the main facts. The reproductive organs proper, the ducts, and the external parts, are developed upon the same plan in male and female. Thus, except in the lowest vertebrates, what serves as an oviduct in the female, is equally present in the embryo male, and persists in the adult as a more or less functionless rudiment. In the same way, what serves as the duct for the sperms (*vas deferens*) in the male is equally present in the embryo female, and persists in the adult as a rudiment, or is diverted to some other purpose. This is a perfectly normal occurrence, dependent upon the embryological history of the ducts in question. It is necessary, however, to realise both the primitive resemblance and the fundamental unity of the two sets of organs, in order to understand how partial hermaphroditism is so frequent, and also to distinguish it from "spurious hermaphroditism," where a merely superficial abnormality or even injury of the ducts in one sex produces a resemblance to those of the other.

We have already mentioned that in the case of twin calves, two females may occur, and both are then normal; or two normal twin calves may be born of opposite sexes; but, in the third place, if both be males, one of these very generally exhibits the peculiar phenomena of what is called a "free-martin." In the commonest form of this, partial hermaphroditism is well illustrated. The essential organs are male, but there is a rudimentary uterus and vagina, and the external organs are further those of a female.

It is necessary to note that a simulation of even this partial hermaphroditism may result from malformation or rudimentary development of the external organs. On this subject we may quote an acknowledged autho-

rity, alike in anatomical and embryological matters. "From the fact," Prof. O. Hertwig remarks, "that the external sexual organs are originally of uniform structure in the two sexes, we can understand the fact that, in a disturbance of the normal development, forms arise in which it is extremely difficult to decide whether we have to deal with male or female external organs. These cases, in earlier times, were falsely interpreted as hermaphroditism. They may have a double origin. Either they are referable to the fact that in the female sex the development may proceed along the same path as in the male, or to this, that in the male the normal development may come at an early age to a standstill, and lead to the formation of structures which resemble the female parts." In the first case, he goes on to say, there may be a simulation of a penis, and the ovaries may even be shifted so as to produce an appearance like that of the testes within their scrotal sac. In the second case, the processes of coalescence which give rise to the penis may not occur, only a rudimentary organ is formed, and there may even be an inhibition of the usual descent of the testes into their sacs.

Of this superficial hermaphroditism, really not hermaphroditism at all, there are numerous cases among mammals. But there remain a large number of recorded instances, where the anatomy of the ducts was predominantly that of the sex opposite to that indicated by the essential organs, and where the combination of the two sexes was also expressed in external configuration and even in habit. Amphibians again furnish some interesting examples. Attached to the anterior end of the testis in various species of toad (*Bufo*), there is an organ known as "Bidder's," which has contents like young ova. These do not, however, get past the early stages, and the organ is quite different from the more than rudimentary ovary which occurs constantly in the males of *Bufo cinereus* and some other species. The two may in fact occur together. In the common frog, dissectors have also recorded several cases of hermaphroditism expressed in the ducts. Lastly, it is perhaps not going too far to include here some reference to the curious "fatty bodies" which occur in all amphibians at the apex of the reproductive organs in both sexes. These appear to nourish the ovary and testis, especially during hybernation, and may perhaps be associated with similar lymphoid structures in fishes and reptiles. Prof. Milnes Marshall demonstrated that the fatty bodies result from the degeneration of the anterior part of the reproductive organ while still in an indifferent state.

Leaving the ducts out of account, we may arrange the important phenomena of hermaphroditism in amphidians in a series as follows:—

(*a*) Embryonic hermaphroditism, demonstrated as of normal occurrence in frog tadpoles.

(*b*) Casual hermaphroditism, demonstrated in frogs, *e.g.* in the occurrence of distinct ova in the seminiferous tubules of *Rana viridis* as reported by F. Friedmann (Arch. Mikr. Anat., lii. (1898), pp. 248-262, 1 pl.

(*c*) Partial hermaphroditism, $\left\{\begin{array}{l}\text{expressed in Bidder's organ in male toads;}\\ \text{(also expressed in various states of the}\\ \text{ducts).}\end{array}\right.$

(*d*) Normal adult hermaphroditism, in some species of *Bufo*.

The list need not be further followed; it is enough to note the very wide occurrence of partial hermaphroditism. In many cases, moreover, we find what may be called superficial hermaphroditism, expressing itself in the external characters. Forms occur in which the minor peculiarities of the two sexes—colouring, decorations, weapons, and the like—appear blended together, or in which the secondary sexual characters are at variance with the internal organs. In most cases, one is safe in saying that there is no true internal hermaphroditism in any degree. Arrest of maturity or puberty, cessation of the reproductive functions, removal or disease of the essential organs, and the like, may alter the secondary sexual characters from female towards male, or, less frequently, *vice versâ*. A female deer may develop a horn, or a hen a spur, and in such cases the ovaries are generally found to be diseased. The prettiest cases of superficial hermaphroditism occur among insects, especially among moths and butterflies, where it often happens that the wings on one side are those of the male, on the other those of the female. Only the external features have been observed in most cases; but it has been shown by dissection that such superficial blending may exist along with internal unisexuality, or, in a few cases, with genuine internal hermaphroditism. A beautiful case of intimate blending of superficial sex characters was lately shown to us by Mr W. de V. Kane of Kingstown. A specimen of butterfly (*Euchloe euphenoides*) showed the anterior half of the fore wings and part of the hind wings with the characteristic white ground of the female, while in the posterior half of the fore wings and on most of the hind wings the characteristic sulphur of the male prevailed. In other minor ways, the characteristics of the two sexes, which are well marked, were intimately blended. In all such cases we may suppose that the imperfection of the normal unisexual differentiation removes the usual limits to the appearance of this or that secondary sexual character.

§ 5. *Normal Adult Hermaphroditism.*—This is rare among the higher animals, but common among the lower. On the threshold of the vertebrate series, we find it indeed constant among the Tunicata; but above these it is very rare. The hag (*Myxine*) was shown by Cunningham, and afterwards by Nansen, to be a protandrous hermaphrodite, but this conclusion is contested by Bashford Dean ("Festschrift Kupffer," 1899). "A testis is constantly found imbedded in the wall of the

ovary in *Chrysophrys* and *Serranus*, and the last-named fish is said to be self-impregnating." In some species of male toad (*e.g.*, *Bufo cinereus*) a somewhat rudimentary ovary is always present in front of the testes. All other cases among vertebrates are either casual (par. 3) or partial (par. 4). Among invertebrates, true hermaphroditism is frequent.

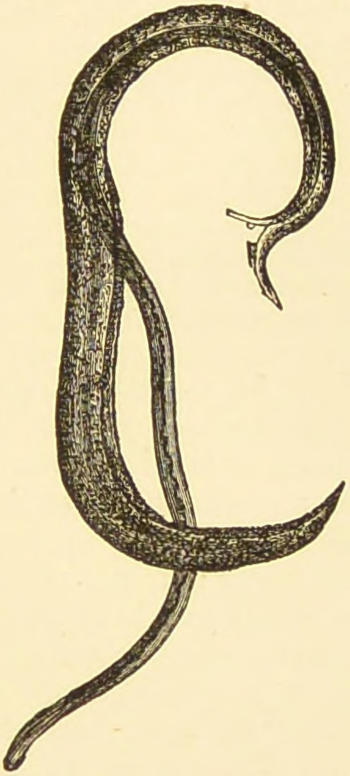
(1.) *Sponges.*—As already mentioned, the sex-cells of sponges arise among the components of the middle layer (*mesoglœa*) of the body. It is at least possible that in *any* sponge they may develop either into ova or into sperms, or into both, within the same organism, according to nutritive and other conditions. The facts, however, are these. Many sponges are only known in a unisexual state, while others are genuinely hermaphrodite. But among the latter it is not uncommon to find (*e.g.*, in *Sycandra raphanus*) that the production of one set of elements preponderates over the other, and thus we have hermaphrodites with a distinctly male or female bias. In other words, they are verging towards unisexuality. It does happen in fact (*e.g.*, in *Oscarella lobularis*) that a species normally hermaphrodite may exhibit unisexual forms.

(2.) *Cœlenterates.*—The members of this class are higher, in having the production of the sex-cells more restricted, to definite regions, tissues, organs, or even "persons." The highly active Ctenophores, like *Beröe*, are all hermaphrodite, and that very closely. On one side of the meridional branches of the alimentary canal ova arise, on the other side spermatozoa. Among sea-anemones and corals the hermaphrodite condition appears in a number of cases, but is sometimes obscured by the fact that the two kinds of elements are produced at different times, corresponding to different physiological rhythms in the life of the organism. The genus *Corallium* (the red coral of commerce) is peculiarly instructive. The whole colony may be unisexual, or one branch of the colony, or only certain individuals on a branch, while genuine hermaphroditism of individual polyps also occurs. Among hydrozoa (zoophytes, swimming-bells, jellyfish), hermaphroditism is a rare exception. The common hydra, which is a somewhat degenerate type, is hermaphrodite, though at the same time individuals may be found with only ovary or only testes. *Eleutheria* is also hermaphrodite, and abortive ova occur in the male of *Gonothyrea loveni*. Sometimes a colony is hermaphrodite (*Dicoryne*), but the stems and individuals unisexual. Sometimes a stem is hermaphrodite, but the individuals unisexual (certain sertularians). Among jelly-fishes the genus *Chrysaora* is known to be hermaphrodite.

(3.) "*Worms.*"—The condition of the sexual organs varies enormously among the diverse types lumped together under the title of "worms" or "Vermes." In the lowly turbellarians, all the genera are hermaphrodite except two, but, as in many other cases, the organs do not reach maturity at the same time, the male preceding. In the related trematodes or flukes, hermaphroditism again obtains, with one exception, or perhaps two. The certain exception is the curious parasite *Bilharzia*, where the male carries the female about with him in a "gynæcophoric canal," formed of folds of skin. In the adjacent class of cestodes or tapeworms, all the members are hermaphrodite, with one alleged exception. The utility of the hermaphrodite state, if the eggs of these parasitic animals are to be fertilised and

the species maintained, can hardly be doubted. It is important to notice too, that self-fertilisation—that is, union of the eggs and sperms of the same organism—has been proved to occur in several trematodes, and seems to be almost universal in cestodes. This may be partly a cause and partly a consequence of the degeneracy of these parasites, for frequent as hermaphroditism is among plants and animals, self-fertilisation is extremely rare.

Hermaphroditism is rare among the free-living nemerteans, but constant in the semi-parasitic leeches. An exception to separateness of the sexes among threadworms or nematodes is found in the curious genus *Angiostomum*. Here, in an organism which is anatomically a female, the reproductive organ begins its activity by producing spermatozoa, which fertilise the subsequent ova. The animal is thus physiologically hermaphrodite, and at the same time self-impregnating. Approaching the higher annelid worms, we find the primitive *Protodrilus* hermaphrodite; the earthworms are constantly so, but all their marine relatives have the sexes separate. The genus *Sagitta*, which stands by itself, is hermaphrodite; the same condition is known as a rarity among the ancient brachiopods (*Lingula*), but is frequent among the colonial Polyzoa. Many, at least, of the Myzostomata—aberrant parasites of Crinoids—are hermaphrodite.



Bilharzia, a parasitic trematode, in which the male carries the female in a special fold of skin called the "gynæcophoric canal."—After Leuckart.

(4.) *Echinoderma.*—Almost all the members of this class have separate sexes. Among the few exceptions are the species of *Synapta* (a divergent Holothuroid), a sand-star (*Amphiura squamata*), and a starfish (*Asterina gibbosa*). The last is particularly interesting. At Roscoff, the individuals are males for one or two years, and then become females; at Banyuls, the individuals are males for at least two or three years, but eventually become females; at Naples some are wholly male, others wholly female, others hermaphrodite impartially, others transitional. (See L. Cuénot, Zool. Anzeiger, XXI., 1898, pp. 273-279, 3 figs.)

(5.) *Arthropods.*—Among crustaceans, hermaphroditism is a rare exception, though it occurs in the majority of the fixed quiescent acorn-shells and barnacles (Cirripedia). There it is associated with the presence of small males, which Darwin called "complemental." The Cymothoidæ (Isopods) show a curious condition somewhat like that of *Angiostomum* above noticed. The sexual organ of the young animal is male, of the old, female in function. In such cases, one must remember the antithesis between the body proper and the reproductive cells. In youth the demands of the body during growth are greater; there is no anabolic surplus to spare, all goes to increase the body. When mature size is reached, and growth and activities are lessened, there is more likelihood of anabolic preponderance in the reproductive, as opposed to the vegetative, system.

Myriopods and insects have always separate sexes, excluding of course abnormal hermaphroditism among the latter.

(6.) *Molluscs.*—Most bivalves are of separate sexes, but exceptions often occur—*e.g.*, in common species of oyster, cockle, clam, &c. In the case of the oyster, the familiar species (*Ostrea edulis*) is hermaphrodite, and a neighbouring species apparently unisexual. In both cases the organs are the same, but in *O. edulis* the same intimate recesses of the reproductive organ produce at one time ova, at another time sperms.

The snails, or gasteropods, are divided into two great groups, according to the twisting of their nerves. The one group (Streptoneura) have the sexes separate; the members of the other series (Euthyneura) are hermaphrodite.

The sea-butterflies, or pteropods, are hermaphrodite, but the elephant's tooth shells (Scaphopods) are unisexual. So in cuttle-fishes (Cephalopods), the sexes are separate.

In the limpet (*Patella*) hermaphroditism occurs as a casual variation, 3 out of 250. The low-level limpets, which are probably better fed, show no preponderance of females, but it may be noted that the female reproductive organ of the limpet is not larger than the male organ, and does not therefore make special demands on nutrition. (See J. F. Gemmill, Anat. Anzeiger, XII., 1896, pp. 393, 394.)

§ 6. *Degrees of Normal Hermaphroditism.*—From what has been already said, it is evident that hermaphroditism may be more or less intimate. Thus the red coral is sometimes female as regards one branch, and male as regards another; a leech has the ovaries far forward, and independent of the long row of testes; in a tunicate the testes and ovary may form one mass, the male cells spreading over the surface of the ovary. In the same way, the organ of a scallop, which exhibits more or less distinct male and female portions, is in a state of less intimate anatomical hermaphroditism than the oyster, where the same cæca of the same organ fulfil both functions *at different times.*

This last caution must be kept in view, for there is throughout, in varying degrees, a tendency to periodicity in the production of male and female elements. Such a want of "time-keeping" between the sexes is called dichogamy, and is one of the conditions which render self-fertilisation rarely possible. The male function has in the majority of cases the precedence. Similarly in flowering plants, although it is not quite accurate to call the stamens the male organs, or the carpels the female organs, it may be said that "protandrous dichogamy" (stamens taking the lead) is very much commoner than "protogynous dichogamy," where the carpels are first matured. This agrees with the curious cases of *Angiostomum*

and Cymothoidæ already mentioned, where the organ was first male and then female, and indeed with at least most cases among closely hermaphrodite animals. Where the male organs are situated in one part of the body, and the female in another, there is less reason against the production of sperms going on at the same time as the production of ova. In terms of our general thesis, protogyny corresponds, like unisexual femaleness, to a relative predominance of anabolism in the life-ratio, and protandry with the reverse.

The common snail (*Helix*) is not only easily dissected, but in the complexity of its arrangements is full of interest. Here, not only are ova and sperms produced within the compass of one small organ, but each little corner of the organ shows female cells forming on the walls and male cells in the centre. It has been suggested by Platner that the outer cells are the better nourished; they therefore naturally become developed into anabolic ova. In the large slug, *Limax maximus*, Babor found a succession of sexual states,—female, hermaphrodite, male, hermaphrodite, female; and suggests that the same alternation may be observed elsewhere. (Verh. Zool.-bot. Ges. Wien, xlviii., 1898, pp. 151-153.)

§ 7. *Self-Fertilisation.*—We have noted above, that though male and female organs be present in the same organism, they tend to become mature at different times, and that the more the closer the seats of formation of the two kinds of elements. It is equally necessary to emphasise that, though both male and female elements may be produced in the same plant or animal, it is probably exceptional for the ovule to be penetrated by a pollen cell from the same flower, and it is certainly rare for an animal to fertilise its own ova.

It is believed by breeders of higher animals that "close-breeding" *beyond a certain point* is dangerous to the welfare of the stock. The offspring tend to be abnormal or unhealthy. In view of this, the rarity of self-fertilisation among hermaphrodites has been explained in terms of the disadvantage of the process. In reality, however, this is putting the cart before the horse. In hermaphrodites, we take it that the two kinds of sexual elements mature and are liberated at different times, not because of any reaction of the disadvantageousness of self-fertilisation on the health of the species, but simply because the simultaneous co-existence of opposite physiological processes is in varying degrees prohibited. More technically, dichogamy is

not a secondary result of the disadvantage of self-fertilisation nor of the advantage of cross-fertilisation, but increasing dichogamy is the primary condition of cross-fertilisation.

Self-fertilisation does, however, occur as an exception among animals,—thus in all probability in the interesting fish *Serranus;* certainly in many parasitic flukes or trematodes; commonly, if not almost always, in tape-worms or cestodes; also in the curious thread-worm *Angiostomum*, and probably in ctenophores, and in some other cases. In regard to some cases, *e.g.*, among hermaphrodite bivalves (where the sperms are usually wafted in with the water), it is impossible as yet to say whether self-impregnation does or does not occur.

Arguing from the bad effects of close breeding among higher animals, Darwin and others have called attention to the numerous contrivances among plants which are said to render self-pollination impossible. In some cases the pollen of a given flower is quite inoperative on the ovule of the same flower, or has the result of producing weakly offspring. There are also many mechanical devices, as the result of which it is difficult or impossible for the pollen of the stamens to reach the stigmas of the flower, or even to be dusted upon them by the unconscious agency of the intruding insects. Moreover, as among animals, so among plants, it is common for the stamens to become mature before the carpels are ready, or, in rarer cases, for the reverse to occur.

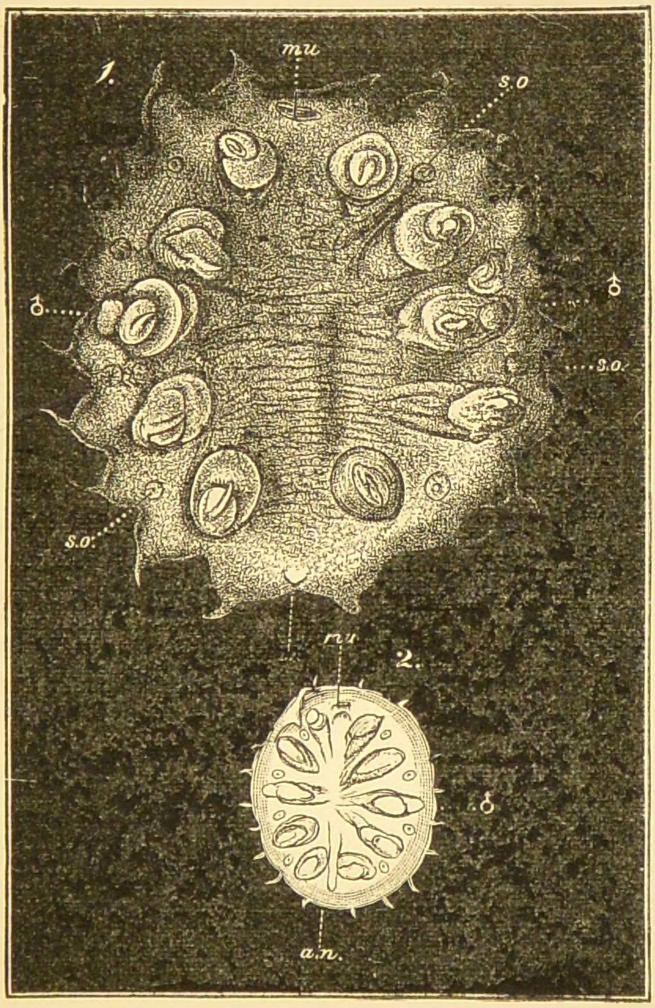
There is no doubt that cross-fertilisation very generally occurs, and it is physiologically probable that this is a considerable advantage, though probably less among plants than among animals. But there is an increasing impression that both the occurrence of cross-fertilisation, and the necessity of it among higher plants, have been exaggerated. One of the most thoughtful and observant of American botanists, Mr T. Meehan, has raised a vigorous protest against the prevalent view. In the *Yucca*, or Adam's needle, which is regarded as cross-fertilised by insects, he showed by experiment that there was in each flower "no abhorrence of its own pollen." "Even when fertilised at all by insects, I am sure the fertilisation is from the pollen of the same flower."

Then as to mechanical contrivances, he says, "we are told that iris, campanula, dandelion, ox-eye daisy, the garden pea, lobelia, clover, and many others, are so arranged that they cannot fertilise themselves without insect aid. I have enclosed

flowers of all those named in fine gauze bags, and they produced seeds just as well as those exposed."

We cannot here enter into a full statement of Meehan's careful observations, but his three main propositions well deserve statement and due consideration:—

1. Cross-fertilisation by insect agency does not exist nearly to the extent claimed for it.



Myzostomata:—(1) A hermaphrodite bearing pigmy males (♂); (2) a pigmy male.—From Nansen.

2. Where it does exist, there is no evidence that it is of any material benefit to the race, but to the contrary.

3. Difficulties in self-fertilisation result from physiological disturbances that have no relation to the general welfare of plants as species.

§ 8. *Complemental Males.*—When Mr Darwin was investigating barnacles and acorn shells, in preparation for his monograph on the group, he discovered the remarkable fact that some of the hermaphrodite individuals carried minute males concealed under their shells. These he regarded as advantageous accessory forms, ensuring cross-fertilisation in the hermaphrodites which harbour them. The great majority of the cirripedes are hermaphrodite; but among the barnacles proper,—the stalked forms, which are nearer the ancestral type, —separate sexes sometimes occur. On the females of a few of these, pigmy males, like those found upon hermaphrodites, also occur. These pigmy males, whether on females or hermaphrodites, are not only dwarfish, but are very often degenerate, sometimes wanting (according to Darwin) both alimentary canal and thoracic legs. Some of them, in fact, are little more than parasitic testes.

The various steps in the evolution may be hypothetically sketched:—

(*a*) The original state of affairs was probably the ordinary crustacean condition of separate sexes. (*b*) A second stage may have been represented by a diminution in the size of the males, as in some of the "water-fleas" or copepods, while the females became more and more sluggish, and settled down. (*c*) In the genera *Alcippe* and *Cryptophialus*, in the species *Ibla cummingii* and *Scalpellum ornatum*, there are true females, with attached pigmy males, often several, leading a shabby existence as parasites. (*d*) In other species of *Scalpellum* and *Ibla* the same pigmy males occur, but attached, as we have noted, to hermaphrodites, which in these forms have replaced the true females. (*e*) Lastly, in many genera, like *Pollicipes*, only hermaphrodites occur.

In a description of the complementary male of *Scalpellum vulgare*, A. Gruvel notes ("Archives de Biologie," xvi., 1899, pp. 27-47, 1 pl.) that it in many respects follows the hermaphrodite form, but is greatly simplified, *e.g.*, in the absence of alimentary canal and of specialised vascular and respiratory organs. He suggests that as the spermatozoa of the hermaphrodite form ripen before the eggs, some of the belated eggs may be fertilised by the spermatozoa of the complementary male which is later in attaining maturity. He supposes further that these belated eggs give rise to the next brood of complementary males. But this, as is the case with so many of these speculations, awaits experimental verification.

What Darwin did for the cirripedes, Graff and others have done for another very curious set of animals, the Myzostomata. These are degenerate chætopods or bristle-footed worms, which occur as outside parasites on sea-lilies (crinoids), on the arms of which they make curious galls. There is unfortunately lack of agreement among observers, and the life-history of these curious forms requires further study. We can only indicate two different sets of results.

According to Beard, "the various kinds of parasitism presented by the

numerous species of *Myzostoma* have led in some cases to the preservation of males, in others to their extinction, in yet others to their conversion into hermaphrodites." He distinguishes—

1. Purely diœcious forms with small males, *e.g.* *M. pulvinar*.
2. Hermaphrodite forms and true males, which remain as dwarf "complemental males" on the back of the hermaphrodites, *e.g.* *M. glabrum*.
3. Hermaphrodite forms and males, which, retaining their position on the back of the others, afterwards become females, *e.g.* *M. alatum*.
4. Hermaphrodite forms, in which the males have lost their dorsal position, and have either become extinct or converted into protandric hermaphrodites, *e.g.* *M. cirriferum*.

According to Wheeler, *Myzostoma glabrum* is from the first hermaphrodite and not dimorphic, but a functional male phase is succeeded by a functional hermaphrodite phase, and that again by a functional female phase during which the testes disappear.

"The cysticolous and endoparasitic species of the genus tend towards a condition in which the functional male and female phases overlap but little, thus exhibiting only a brief hermaphrodite phase (*M. eremita*), or these phases no longer overlap and thus present two well-marked periods of sexual maturity, one male and the other female (*M. pulvinar*)."

§ 9. *Conditions of Hermaphroditism.*—A review of the occurrence of normal hermaphroditism suggests few general conclusions. Claus points out that hermaphroditism finds most abundant expression in sluggish and fixed animals. Flukes, tapeworms, leeches, even earthworms and land-snails, may illustrate the sluggard hermaphrodites; among sponges, sea-anemones, corals, Polyzoa, bivalves, &c., we find frequent illustration of the association of fixedness and hermaphroditism. Most of the tunicates are also fixed, and all are hermaphrodite. But the pelagic tunicates are also hermaphrodite, and so are the very active Ctenophora. Claus notes further that in flukes and tapeworms hermaphroditism is associated with an isolated habit of life. But there is often anything but isolation, for flukes may occur near one another in great numbers; and as many as ninety tapeworms (*Bothriocephalus*) have been known to occur at one time in a single host.

Simon has gone further, in insisting on the physiological connection between quiescent and parasitic habit and the hermaphrodite condition. In flukes and tapeworms, leeches, Myzostomata, and some cirripedes, we find the association of hermaphroditism with a more or less intimate parasitic habit. But what Simon points out is, that organisms on which great demands are made, especially in the way of muscular exertion,

cannot afford to be hermaphrodite; while a plethora of nutrition, as in parasitism, tends to make the persistence of the double state possible. He gives numerous illustrations in support of this view. Others are content to interpret the hermaphroditism in all these cases as an *adaptation* to ensure fertilisation, for the possibilities of pairing between separate sexes are certainly lessened if the animals are sluggish, sedentary, or parasitic.

§ 10. *Origin of Hermaphroditism.*—(1) One view of the matter is that hermaphroditism was the primitive state among multicellular animals, at least after the differentiation of sex-elements had been accomplished. In alternating rhythms, eggs and sperms were produced. The organism was alternately male and female. Of this primitive hermaphroditism, there may be more or less of a recapitulation in the life-history of the organism. Gegenbaur states the common opinion in the following cautious and terse words:—"The hermaphrodite stage is the lower, and the condition of distinct sexes has been derived from it." Unisexual "differentiation, by the reduction of one kind of sexual apparatus, takes place at very different stages in the development of the organism, and often when the sexual organs have attained a very high degree of differentiation." The first structural stage in the separation would probably be the restriction of areas, in which the formation of two kinds of cells still went on at different times in one organism. In different individuals the opposite tendencies we have already spoken of more and more predominated, till unisexuality evolved out of hermaphroditism.

That environmental conditions are effective in changing the hermaphrodite into the unisexual state is suggested by many experiments. And it has been shown in regard to some flowering plants, *e.g.* butcher's broom (*Ruscus aculeatus*), that the monœcious or diœcious condition may be evoked by altering the nutritive conditions.

(2) Quite different is the view which regards hermaphroditism as a secondary condition, derived from primitive unisexuality. Thus Pelseneer maintains that the "study of Mollusca, Myzostomidæ, Crustacea, and Pisces shows that in these groups the separation of the sexes preceded hermaphroditism; various cases in other groups tend to show that this is true universally; and the same conclusion applies to plants. In Mollusca, Crustacea, and Pisces, at least, hermaphroditism is grafted upon the female sex."

SUMMARY.

1. Hermaphroditism is the union of the two sexual functions in one organism. This occurs, however, in varying degrees.

2. Embryonic hermaphroditism is probably a general fact with even unisexual animals. It is certain in some cases.

3. Casual or abnormal hermaphroditism is not infrequent.

4. Partial hermaphroditism (not involving the essential organs) is exceedingly common.

5. Normal adult hermaphroditism; review of its occurrence.

6. True hermaphroditism occurs in many degrees of intimacy.

7. Self-fertilisation is a rare exception among animals; commoner in plants.

8. "Complemental males" — pigmies attached to hermaphrodites—occur in two groups.

9. The conditions of hermaphroditism. Commonest in sedentary, sluggish, parasitic forms.

10. Hermaphroditism is primitive; the unisexual state is a subsequent differentiation. *Or*, Unisexuality is primitive; the hermaphrodite state secondary. Possibly both suggestions may be true.

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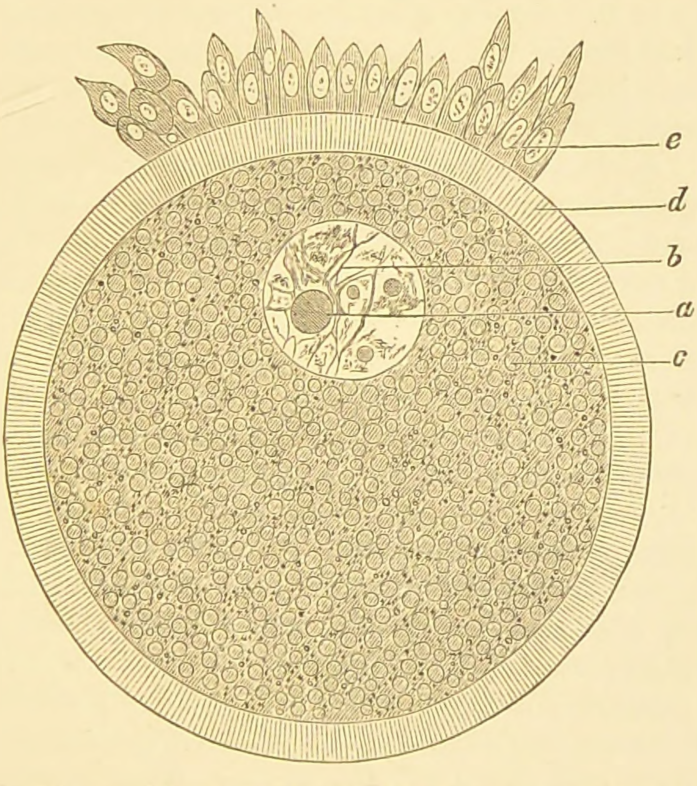
CHAPTER VII.

The Ultimate Sex-Elements (*General and Historical*).

In our analysis of sex-characters we have followed the general course of biological history. We first passed from the form and habit of a male or female *organism* to the structure and functions of the sexual *organs*. In discussing hermaphroditism, we had occasion to refer to a third step of biological analysis, that which involves an investigation of the properties of the



Mammalian ovum, showing nucleolus (*a*), nucleus (*b*), cytoplasm (*c*), external porous zone or zona pellucida (*d*), and follicular cells (*e*). —From Hertwig, after Waldeyer.

tissues. Now it is necessary to penetrate deeper, namely, to the *sex-cells*. After these have been considered we shall be in a better position to re-ascend to some of the problems of reproduction.

§ 1. *The Ovum Theory.*—It is now a commonplace of observation and established fact, that all organisms, reproduced in the ordinary way, start in life as single cells. We see insects laying their ova upon plants, or fishes shedding them in the water, and may watch how these cells, provided they be fertilised, give rise eventually to the adult organisms. Conveniently in the ordinary frog-spawn from the ditch, we can read, what was for so long a riddle, how development proceeds by successive cell-divisions and by arrangement of the multiple results. Readily seen in many instances, it is true of all cases of ordinary sexual reproduction, that the organism starts from the union of two sex-cells. In other words, it is with the division of a fertilised ovum that development begins.

This profound fact, technically known as the "ovum theory," has been not unjustly called by Agassiz "the greatest discovery in the natural sciences of modern times." We shall the better realise the magnitude of the difference which its recognition has introduced into biology, if we briefly review the history.

§ 2. *The History of Embryology: Evolution and Epigenesis.*—The development of the chick, so much studied in embryological laboratories to-day, was the subject of inquiry two thousand years ago in Greece. Some of the conspicuous marvels of reproduction and development were the subjects of persistent but fruitless speculation throughout many centuries. It was only during the scientific renaissance of the seventeenth century that the inquiry became more keen and precise, and began to rely to some extent at least on genuine observation.

(*a*) Harvey (1651), with the aid of magnifying glasses (*perspecillæ*), demonstrated in the fowl's egg the connection between the *cicatricula* of the yolk and the rudiments of the chick, and also observed some of the stages of uterine life in mammals. More important, however, were his far-sighted general conclusions,—(1.) That every animal was produced from an ovum (*ovum esse primordium commune omnibus animalibus*); and (2.) That the organs arose by new formation (*epigenesis*), not from the mere expansion of some invisible preformation. In this generalisation, without however any abandonment of the hypothesis of spontaneous generation of germs, he strove, as he said, to follow his master Aristotle, and was in so doing as far ahead of his contemporaries as a strong genius usually is. Before Harvey, the observational method had

indeed begun. Thus, as Allen Thomson notes, Volcher Coiter of Groningen (1573), along with Aldrovandus of Bologna, had watched the incubated egg in its marvellous progress from day to day. Fabricius ab Aquapendente (1621) had also studied the changes in the incubated egg, and the stages of the mammalian fœtus. In keenness of vision, Harvey was far ahead of these.

(*b*) Malpighi (1672), using a microscope with phenomenal skill, traced the embryo back into the recesses of the cicatricula or rudiment, but again missed a magnificent discovery, and supposed the rudiments to have pre-existed in the egg. In 1677, Leeuwenhock was led by Hamm to the discovery of the spermatozoa; and this was followed up, though not to much profit, by Vallisneri and others. Steno, too, in 1664, had given the ovary its present designation; and De Graaf had interpreted the vesicles of this organ, which now bear his name, as for the most part equivalent to the ova which he had discovered in the oviduct. Needham (1667), Swammerdam (1685), and J. van Herne, also contributed items of information not then appreciated in their real relations.

(*c*) *The Theory of Preformation—Ovists and Animalculists.* —In the early part of the eighteenth century, the embryological observations of investigators, *e.g.* Boerhaave, were summed up in the conception that development was merely an expansion or unfolding of a pre-existent or preformed rudiment within the egg. Harvey had indeed striven for an opposite conclusion, but his view was negatived, as we have seen, by Malpighi's failure to trace the embryo beyond the rudiments of the cicatricula.

The notion of a preformed rudiment, thus suggested by Boerhaave, Malpighi, and others, rapidly became the prevalent theory. In so far as it emphasises one side of the facts, it is bound in modified form so to remain. Leibnitz, Malebranche, and others found it to fit in better with their cosmic conceptions than the older view of Aristotle had done, and welcomed it accordingly.

The positions occupied by the physiologist Haller well illustrate the alterations of opinion. As Allen Thomson points out in his article "EMBRYOLOGY," in the *Encyclopædia Britannica*, "Haller was originally educated as a believer in the doctrine of 'preformation' by his teacher Boerhaave, but was soon led to abandon that view in favour of 'epigenesis' or

new formation. But some years later, and after having been engaged in observing the phenomena of development in the incubated egg, he again changed his views, and during the remainder of his life was a keen opponent of the system of epigenesis, and a defender and exponent of the theory of 'evolution,' as it was then named."

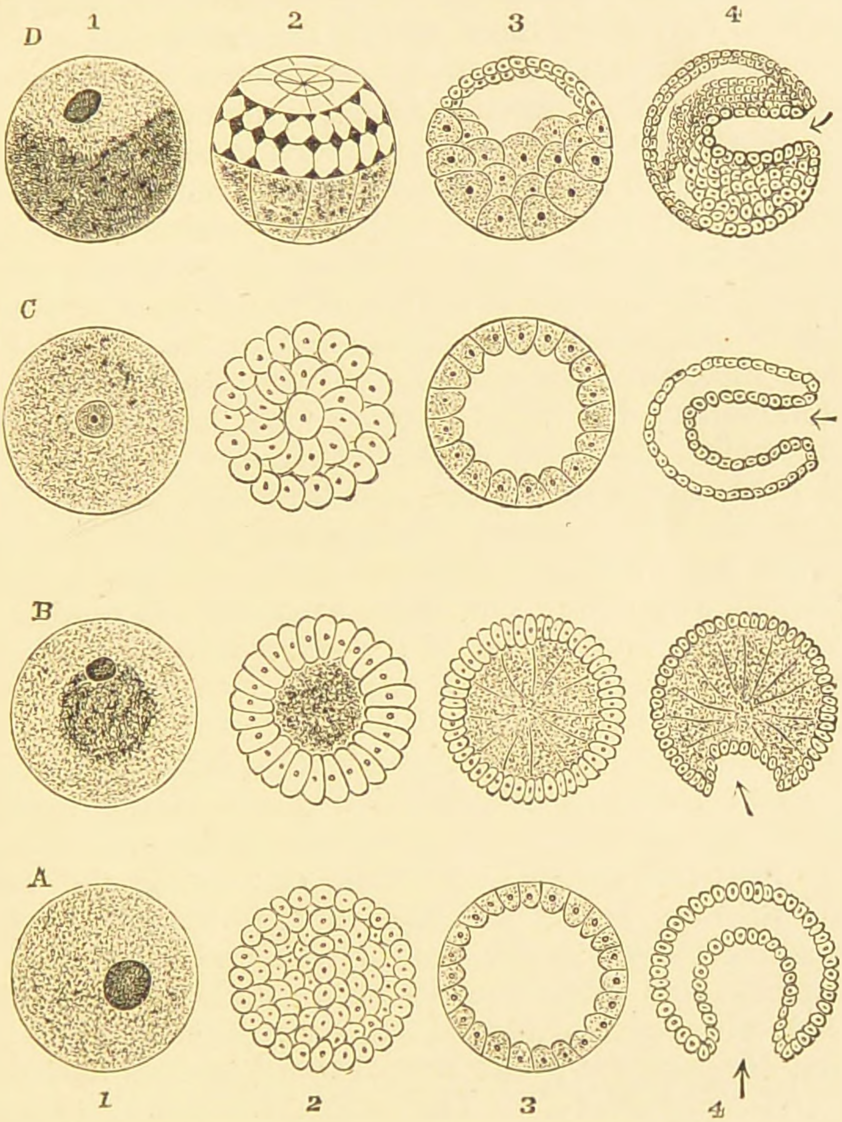
The preformation theory found more and more definite expression in the works of Bonnet, Buffon, and others. It is now necessary to sum up its main propositions.

The germ, whether egg-cell or seed, was believed to be a miniature model of the adult. "Preformed" in all trans parency the organism lay within the egg, only requiring to be unfolded. Many affirmed, that before fertilisation there lay within the fowl's ovum an excessively minute but complete chick. They compared the germ to a complex bud, which hides within its hull the floral organs of the future. Harvey had said, "the first concrement of the future body grows, gradually divides, and is distinguished into parts; not all at once, but some produced after the others, each emerging in its order." Very different was Haller's first and last utterance, "There is no becoming; no part of the body is made from another, all are created at once." This was obviously a short and easy method with embryology, if the organism was literally preformed in the germ, and its development simply a growth and an unfolding.

But this was not all. The germ was more than a marvellous bud-like miniature of the adult, it necessarily included in its turn the next generation, and this the next—in short all future generations. Germ within germ, in ever smaller miniature, after the fashion of an infinite juggler's-box, was the corollary logically appended to this theory of preformation and unfolding,—of *evolution*, as it was then called, in a very different but more literal sense from that in which we now use the word.

A side controversy of the time arose between two schools, who called each other "ovists" and "animalculists." The former maintained that the female germ element was the more important, and only required to be as it were awakened by the male element to begin the process of unfolding. The animalculists, on the other hand, asserted the claims of the sperm to be the bearer of the miniature nest of organism within organism, and supposed that it only required to be fed by the ovum to enlarge and unfold the first of the models which it concealed.

(*d*) *Wolff's Reassertion of Epigenesis.*—The above ingenious construction was rudely shaken down, however, in 1759, when Caspar Friedrich Wolff showed, in his doctorial dissertation, the illegitimacy of the suppositions which lay at the root of the



The first stages of development in a number of animals. *A*, Sponge, Coral, Earthworm, or Starfish; *B*, Crayfish or other Arthropod; *C*, Tunicate, Lancelet, &c.; *D*, Frog or other Amphibian.
1. Fertilised ovum; 2. Segmented ovum, a ball of cells, morula, or blastosphere; 3. The same, after further division or in section; 4. The gastrula stage.

preformation theory. He traced the chick back to a layer of organised particles (the familiar *cells* of to-day), in which there was no likeness of the future embryo, far less adult. More

than that, he followed the disposition of these primitive elements to the upbuilding of some of the important organs. He undoubtedly reacted too far in his emphasis on the entire simplicity of the germ, and many of his details were mistaken; but none the less did he recall embryologists from speculation to take the facts as they found them, and lay the foundation of modern embryology in the fact that there is an observable process of development from the apparently simple to the obviously complex.

(*e*) *Wolff's Successors.*—The important conclusion reached by Wolff remained for about sixty years without effect. In 1817, Christian Pander took up embryological research exactly where Wolff had left it, and worked out the history of the chick in more exact detail. In 1824, Prévost and Dumas noticed the division of the ovum into masses; and in the following year Purkinje discovered the nucleus or "germinal vesicle." Von Baer followed up his friend Pander's work, and in 1827 made the memorable discovery of the mammalian ovum, which he traced from uterus to oviduct, and then to its position in the ovary itself. Thus, after a century and a half, De Graaf's endeavour was at length fulfilled. Soon afterwards, Wagner, von Siebold, and others, elucidated what was still hidden from von Baer,—the real nature of the spermatozoa. Meanwhile, Bichât's analysis (1801) of the organism into tissues, was with improved appliances deepened in the casual description of "cells"; and an important generalisation had its forecast in 1835, when Johannes Müller pointed out in the vertebrate notochord the existence of cells resembling those of plants.

§ 3. *The Cell-Theory.*—Without continuing the history further, we must simply note that in 1838 Schleiden referred all vegetable tissues to the cellular type, and traced back the plant embryo to a single nucleated cell; while, in the following year, Schwann boldly extended this conception of plant structure and development to the animal world, and so fully constituted the "cell-theory." The ovum, recognised as a cell, became a "primordium commune" in a deeper sense than Harvey dreamt of; the masses described by Prévost and Dumas were seen as the products of cell division; and Kölliker led the way, now so well followed up, in tracing these cells to their results in the tissues of the organism

§ 4. *Protoplasmic Basis.*—Only one step further is it possible for biological analysis to penetrate, and that within the last few years is being persistently essayed. It is impossible to rest at

the cell-theory level. To recognise the ovum as a cell, and the spermatozoon as another, to find the starting-point of the organism in the double unity formed from these two, to demonstrate the process of development as one of cell multiplication and arrangement, express great but not final biological facts. Thus it is that of late years, what Michael Foster has called the "protoplasmic movement" has made itself felt, not only in study of the general functions of the body, but in the special physiology of the reproductive cells and their history. Even in morphological or structural studies, attention has shifted from the shapes of cells to the structure of their living matter, or from the different forms of ovum and spermatozoon to the germinal protoplasm or Keimplasma which they contain. On

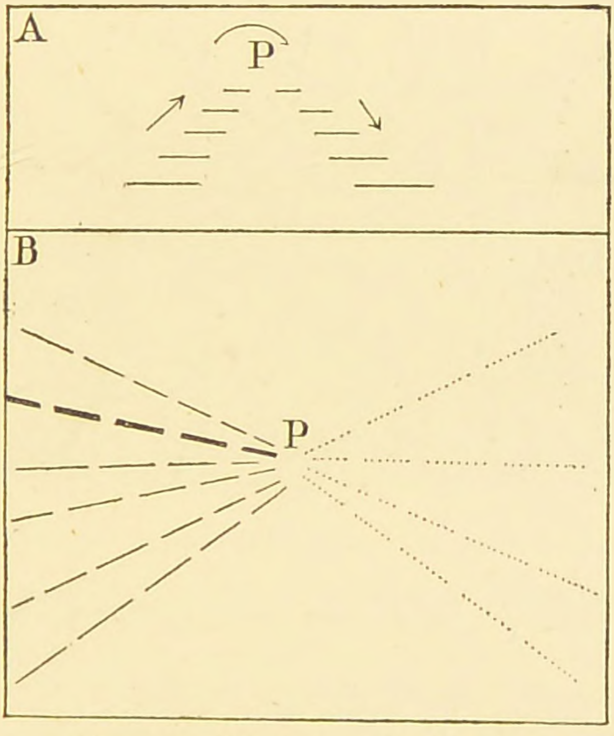
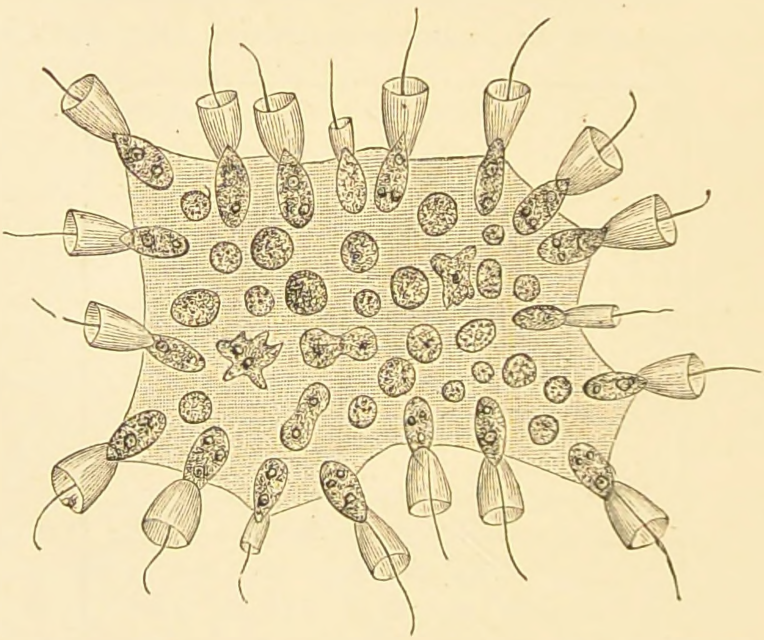


Diagram of Protoplasmic Changes. B in plan, A in elevation.

this level, in fact where biology has touched the bottom, morphology and physiology have become more than ever inseparable. All the facts of structure on the one hand, and of function on the other, have both to be interpreted in terms of the constructive and disruptive changes in the living matter itself. The general theory may be summarised in the accompanying diagram. Protoplasm is regarded as an exceedingly complex and unstable compound, undergoing continual mole-

cular change or metabolism. On the one hand, more or less simple dead matter or food passes into life by a series of assimilative ascending changes, with each of which it becomes molecularly more complex and unstable. On the other hand, the resulting protoplasm is continually breaking down into more and more simple compounds, and finally into waste products. The ascending, synthetic, constructive series of changes are termed "anabolic"; and the descending, disruptive series, "katabolic." Both processes may be manifold, and the predominance of a particular series of anabolic or katabolic changes implies the specialisation of the cell.



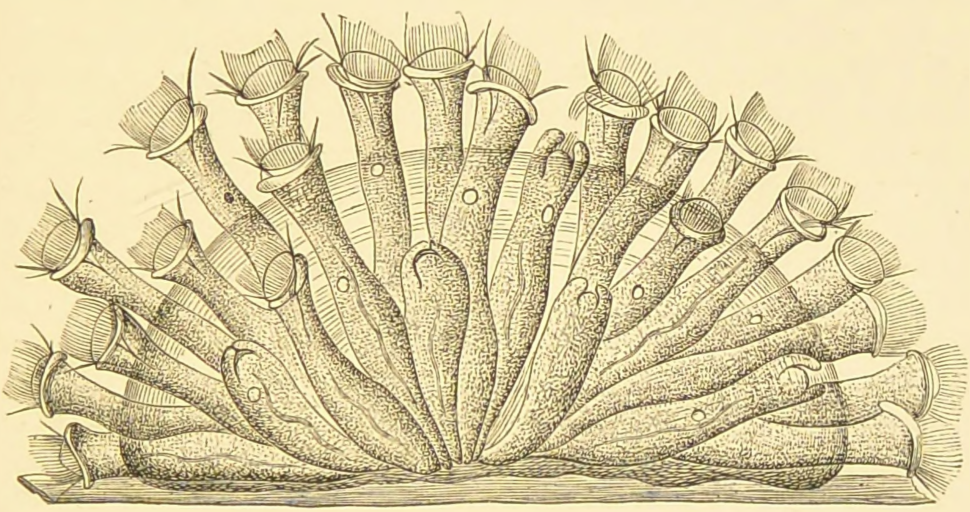
Proterospongia, a colonial infusorian, showing the difference between outer and inner cells.—From Saville Kent.

The figure (A, on p. 93) represents the complex unstable protoplasm as if occupying the summit of a double flight of steps; it is formed up the anabolic steps, it breaks up and descends by the katabolic. The lower figure (B) is a projection of the other, its convergent and divergent lines serving to represent the various special lines of anabolism and katabolism respectively, and the definite component substances ("anastates" and "katastates") which it is the task of the chemical physiologist to isolate and interpret.

From a general physiological point of view it matters little if we make a slightly different assumption, namely, that protoplasm does not exactly share in the twofold process of metabolism, but is a substance *per se*, acting, like a ferment, on the complex materials around it. Even if we suppose, as some do, that there is no such substance as protoplasm, life being the

expression of the inter-relations of many complex substances, still, the two main aspects of metabolism—anabolic and katabolic—remain.

§ 5. *Protozoa and Metazoa.*—It has been emphasised above that every multicellular organism, reproduced in the ordinary way, starts from a fertilised ovum, from what may be fairly called a single cell. Sponge, butterfly, bird, and whale begin, in a sense, at the level of the simplest animals or Protozoa, which (with the exception of some which form colonies) remain always unicellular. The simplest organisms leave off where the higher plants and animals begin, *i.e.*, as single corpuscles of living matter. They correspond, in fact, to the reproductive cells of higher animals, and may be called, according to



Ophrydium, a colonial infusorian.—From Saville Kent.

their predominant character, protova and protosperms. A fertilised ovum, as we have seen, proceeds by division to form a "body"; the Protozoon remains, with few exceptions, a single cell, in which there is obviously no distinction between reproductive elements and the entire organism.

Reference will have to be made to the Protozoa in three connections, which may be here simply noted:—

(*a*) In their chief groups, and in the stages of their life-histories, they express phases in the same cell cycle which recurs in higher forms in the component elements of the body, and in the reproductive cells. The contrast, in other words, between an infusorian and an amœba, between the ciliated

and amœboid stage in the life-history of many forms, is a forecast of the contrast between a ciliated cell and a white blood corpuscle, between a mobile spermatozoon and a young ovum. A predominance of the same protoplasmic processes is the basal interpretation of the similarities of form.

(*b*) It is among the Protozoa that we must look, if we hope to understand the origin and import either of "male and female," or of fertilisation.

(*c*) Among the loose colonies which some Protozoa form, and which bridge the gulf between the unicellular animals and the Metazoa, there is seen the beginning not only of the formation of a "body" (see figs. on pp. 94, 95), but also the setting apart of special reproductive cells. On this point more emphasis must be laid. The ordinary Protozoon is a single cell, and forms no body. It divides indeed, and multiplies accordingly, but the products of division go asunder, whereas in the segmentation of the ovum they remain connected. In most Protozoa, there is continual self-recuperation; in most, division occurs without any loss; in most, there is no distinction between parent and offspring; in most, as there is no body, there is no death. Thus it is that, with one weighty caution to be afterwards noted, it seems justifiable to speak with Weismann and others of the "immortality of the Protozoa." In a certain sense too, as we shall see, it is justifiable to speak of the immortality of the reproductive cells in higher animals. The body dies, but the reproductive cells escape, before its death, to live on, as new organisms, enclosing new sets of reproductive cells. Again there is similarity between the Protozoa and the reproductive cells.

But in some of the loose colonies (*e.g.*, *Volvox*), we see the beginning of the change which introduced death as a constant phenomenon (see fig. p. 139). The cell, which starts one of these colonies, divides; the products of division, instead of going apart as usual, remain connected; a loose body of many cells is thus formed. In this cluster of cells, certain elements are in turn set apart and eventually adrift, as reproductive cells. They start new colonies, and thus we are introduced to what is constant in higher animals. The only marked differences are—(*a*) that the body of the Metazoon is more than a loose colony of cells; (*b*) that the reproductive elements are usually liberated from some definite region or organ; and (*c*) that they are more markedly differentiated as male and female cells.

§ 6. *General Origin of the Sex-Cells.*—Except in the lowest invertebrates, the sponges and cœlenterates, the reproductive elements almost always arise in connection with the middle layer (mesoderm or mesoblast) of the body.

Neither in sponges nor in cœlenterates is there a middle layer exactly comparable to the mesoderm of higher animals; the less definite middle stratum is now frequently termed a mesoglœa. In sponges, we already mentioned that the reproductive cells simply arise here and there among the other elements of the stratum. The ova are highly nourished mesoglæal cells; the primitive male cells, which divide into numerous minute spermatozoa, are the reverse.

In cœlenterates the phenomena are of much interest; the origin of the sex-cells is very diverse. Some time ago considerable emphasis was laid, by E. van Beneden and others, on the fact that, in certain Hydrozoa, "the ova are derived from the endoderm, and the sperms from the ectoderm." Thus Gegenbaur, accepting this, remarks that in such cases "the endoderm is the female, and the ectoderm the male germinal layer." Such a generalisation, if established, would be plausible enough, seeing that the inner or endoderm layer is the more nutritive or anabolic of the two. A controversy, however, soon arose, the result of which was to overthrow the generalisation. In hydra, we have already noticed that both products arise from the ectoderm; the same was shown by Ciamician to be true of *Tubularia mesembryanthemum;* while in the *Eudendrium ramosum* the ova appeared to arise from the *ectoderm*, and the male elements from the *endoderm*, the very reverse of Van Beneden's conclusion. The matter was settled, so far as the general facts are concerned, by Weismann, who established the fact of active migration of the elements from one layer to another. He has since been followed by other investigators. (*a*) The sex-elements, both male and female, may appear first in the endoderm, whether they originate there or not, and from this inner layer they migrate to the ectoderm, where they ripen. (*b*) In rare cases they even ripen in the endoderm. (*c*) Very commonly the sex-cells originate in the ectoderm and ripen there, or they may pass thence into the endoderm and back again to the ectoderm. (*d*) In the medusa of *Obelia*, the ova appear to ripen partly in both layers. These facts, a convenient summary of which will be found in Hatchett Jackson's erudite edition of Rolleston's "Forms of Animal Life," show plainly enough how varied are the origin and history of the sex-cells in these forms.

The colonial hydroids typically produce well-marked reproductive individuals or sexual zooids, set free as "swimming-bells" or medusoids (in a process to be afterwards described under "Alternation of Generations"). In these the reproductive elements are typically developed. But in varying degrees these medusoids have degenerated, and are frequently not only not liberated, but lose their characteristic features, and become mere reproductive buds. In these buds the sex-cells are normally developed. But it very frequently happens that they arise more or less in the body of the asexual vegetative hydroid. They ripen early, and subsequently migrate to their proper place; the asexual stage incorporating more and more of the originally separate sexual generation. Weismann has emphasised the value of this early ripening as an advantage to the race,

lessening the danger of its extinction; and this has doubtless to be considered. But important as all such considerations are, they cannot dispense with an enquiry into the physiology of the facts.

§ 7. *Early Separation of Sex-Cells.*—Having noted the general fact of mesodermic origin, and some of the interesting phenomena observed in cœlenterates, we shall not further pursue the subject except as regards one question, the period at which the reproductive cells make their appearance. This is sometimes early, sometimes late; and it is not yet decisively known in how many cases early separation occurs, nor how far the fact is of much significance.

In the case of a well-known fly, *Chironomus*, Professor Balbiani, unprejudiced by any theory of heredity, observed the following facts:—Before the segmentation of the egg had at all advanced, before what embryologists call the blastoderm was more than incipient, two cells were observed to be set apart externally. (These had nothing whatever to do with the polar globules seen in most ova at maturation.) The development proceeded apace, but the isolated cells took no share; they may be presumed to have retained intact the characters which they received when first divided off from the ovum. At a certain stage, however, the isolated cells sank inwards, took up an internal position, became the rudiments of the reproductive organs. Here then, at an early stage, before differentiation is marked, the reproductive cells are set apart. They must therefore preserve much of the character of the parent ovum, and hand on the tradition intact by continuous cell-division to the next generation.

In other words, in the preceding case, at a very early stage in the embryo, the future reproductive cells are distinguishable and separable from the body-forming cells. The latter develop in manifold variety, into skin and nerve, muscle and blood, gut and gland; they differentiate, and lose almost all protoplasmic likeness to the mother ovum. But the reproductive cells are set apart; they take no share in the differentiation, but remain virtually unchanged, and continue unaltered the protoplasmic tradition of the original ovum. After a while they, or their division-products rather, will be liberated as reproductive cells. These in a sense will be continuous with the parental germ. Their protoplasm will be more or less identical. The original ovum has certain characteristics, *a b c x y z;* it divides, and all its cells must at first more or less share these characteristics;

the body-cells lose some of them, the insulated reproductive cells retain them all. The ovum of the next generation has thus also the characteristics *a b c x y z*, and must therefore produce an organism essentially like the parent.

An early isolation of the reproductive cells, though rarely so striking as in *Chironomus*, has been observed in many cases,—*e.g.*, in some other insects, in the aberrant worm-type *Sagitta*, in leeches, in threadworms, in some Polyzoa, in some small crustaceans known as Cladocera, in the water-flea *Moina*, in the parasitic Hymenopteron *Platygaster*, in some arachnoids (Phalangidæ), in the bony fish *Micrometrus aggregatus*. As the series is ascended, the reproductive organs seem to be later in making their appearance, at least they are only detected at a later stage. It must also be pointed out that, in cases of alternation of generations, an entire asexual generation, or more than one, may intervene between one ovum and another.

Perhaps the most striking of all the cases of the early segregation of the lineage of germ-cells is that described by Boveri in *Ascaris megalocephala*, the threadworm of the horse. He was able to trace back the germ-cells continuously to the two-cell stage. At the very first cleavage the distinction between somatic and reproductive is established. One of the first two cells is the ancestor of all the cells of the body; the other is the ancestor of all the germ-cells. " Moreover, from the outset the progenitor of the germ-cells *differs from the somatic cells not only in the greater size and richness of the chromatin of its nucleus but also in its mode of mitosis*, for in all those blastomeres destined to produce somatic cells a portion of the chromatin is cast out into the cytoplasm, where it degenerates, and *only in the germ-cells is the sum-total of the chromatin retained.*"—(E. B. Wilson, "The Cell in Development and Inheritance," 1896, p. 111.)

§ 8. *Body Cells and Reproductive Cells.*—Various naturalists have insisted on the contrast hinted at above, between the cells of the embryo which go to form the body and those which are set apart as reproductive organs.

(*a*) As early as 1849, Owen noted that, in the developing germ, it was possible to distinguish between cells which became much changed to form the body, and cells which remained little changed and formed the reproductive organs. This view, as Brooks points out, he unfortunately afterwards departed from in his "Anatomy of the Vertebrates."

(*b*) In 1866, Haeckel connected reproduction with discontinuous growth, and insisted upon the material continuity between parent and offspring. Somewhat later, both he and Rauber drew a clear contrast between the somatic and reproductive elements, between the "personal" and "germinal" portions of the embryo, or between the body and the sex cells.

(*c*) W. K. Brooks, in 1876 and 1877, again drew attention to this significant contrast.

(*d*) Yet more explicit, in 1877, was the ingenious Dr Jäger, now better known in a very different connection, and a few of his sentences well deserve to be quoted. Referring to a previous paper, he writes as follows:—"Through a great series of generations, the germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic portion, out of which the individual is built up, and a phylogenetic portion, which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as *the continuity of the germ-protoplasm.* Encapsuled in the ontogenetic material, the phylogenetic protoplasm is sheltered from external influences and retains its specific and embryonic characters."

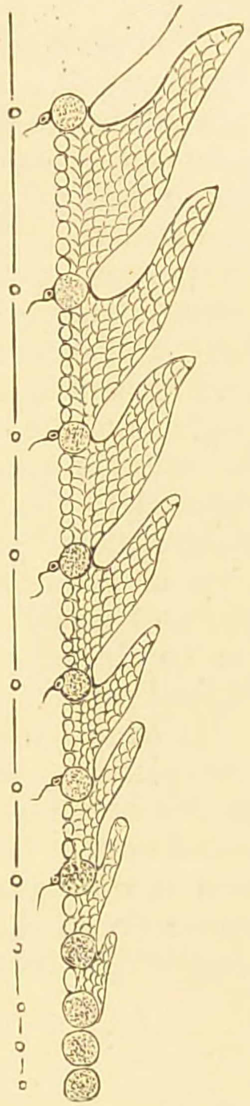
(*e*) In an exceedingly clear manner, to which sufficient attention seems hardly to have been accorded, Galton, in 1876 and at other dates, as again more indirectly in his work on "Natural Inheritance," drew attention to the contrast between the gemmules of the ovum (stirp) which go to form the body, and those which, remaining undeveloped, form the sex-cells. "The developed part of the stirp is almost sterile" (*i.e.*, without influence in heredity); "it is from the undeveloped residue that the sexual elements are derived."

(*f*) Lastly, in 1880, Nussbaum, in an elaborate investigation on the differentiation of the reproductive cells, drew emphatic attention to some cases of their early separation, and reasserted Jäger's conception of a continuity of germ-protoplasm. In this survey, however, we do not pretend to decide the difficult question of priority in the enunciation of this conception. Like many other generalisations, it appears to have arisen all but simultaneously in many minds.

(*g*) It is to Weismann, however, that biology is particularly indebted for his vindication and elaboration of the doctrine of genetic continuity.

§ 9. *Weismann's Theory of the Continuity of the Germ-*

Protoplasm.—In some cases referred to in a foregoing paragraph, it is possible to trace a direct cellular continuity, first of all, between the ovum and early separated reproductive rudiments, secondly, between the latter and the future ova and sperms. There is not only cellular continuity between the ovum which gives rise to parent, and the ovum which gives rise to offspring,—that the cell-theory demands,—but there is a continuity in which the character of the original ovum is never lost by differentiation. In fact, there is a continuous chain of reproductive cells quite apart from the body cells. It is in this sense that some of the authors quoted have spoken of the continuity of the germ-*cells*. This is certainly true for some cases. If it were true for all, the problems of reproduction and heredity would be much simpler than they at present appear to be.



The relation between reproductive cells and the body. The continuous chain of basal cells at first represents a succession of Protozoa; further on, it represents the ova from which successive "bodies" are produced. At each generation, a spermatozoon fertilising the liberated ovum is also indicated.

For in the present state of our knowledge we can only speak of the continuity of the reproductive *cells*, in exceptional or rather in a small minority of cases. Alike in the higher vertebrates and the lowly hydroids, the reproductive cells may appear late. After the differentiation of the vertebrate embryo has progressed far, or the life of the polyps continued for long, the germ-cells make their appearance; and though we know of course that they are descendants of the original ovum, yet we must allow, with Weismann, that in the form of special cells they are now for the first time to be detected. Therefore, Weismann says, "a continuity of germ-*cells* is now for the most part no longer demonstrable."

Yet there is nothing that Weismann more strongly insists upon, than the reality of continuity between ovum and ovum. In what does it consist, if a chain of ovum-like cells is only true of a minority of organisms? It consists,

according to Weismann, in the "Keimplasma" or germ-plasm.

The germ-plasm is the distinctive part of the nucleus of the germ-cell. It has an extremely complex, and at the same time persistent, structure. It is the substance which enables the germ-cell to build up an organism; it is the architectural living matter, and the immortal bearer of all properties transmitted in inheritance. "In every development," according to Weismann, "a portion of this specific germ-plasm, which the parental ovum contains, is unused in the upbuilding of the offspring's body, and is reserved unchanged to form the germ-cells of the next generation. . . . The germ-cells no longer appear as products of the body, at least not in their most essential part—the specific germ-plasm; they appear rather as something opposed to the sum-total of body-cells; and the germ-cells of successive generations are related to one another like generations of Protozoa." But the continuity is rarely kept up by a chain of undifferentiated reproductive *cells;* it depends upon the continuance and unchanged persistence of part of the original *germ-plasm.*

It need hardly be pointed out that the conception of the germ-plasm is theoretical. For just as we cannot point to any one portion of the cell and say this is *protoplasm—the* living matter—and nought else; so we cannot demonstrate the *germ-plasm*, even if we accept the current view that it has its basis in the chromatin of the nucleus. The theory is a conceptual interpretation, and must be tested by its power of fitting facts.

SUMMARY.

The progressive analysis through organism, organs, tissues, and cells, to the living matter itself.

1. The Ovum-theory.—Every multicellular organism, reproduced in the ordinary way, arises from a fertilised egg-cell, and development proceeds by cell-division.

2. Epigenesis and Evolution.—History of the different views taken of the development of the organism; ancient speculations. The scientific renaissance. (*a*) Harvey's prevision of the ovum-theory, and emphasis upon "epigenesis." (*b*) Observations of Malpighi and others, mostly against Harvey's view. (*c*) The theory of preformation,—of a nest of miniature models within the egg, only requiring to be unfolded in successive generations; Ovists *versus* Animalculists. (*d*) Wolff's reassertion of "epigenesis," the foundation of modern embryology; his exaggeration of the simplicity of the germ. (*e*) Wolff's successors.

3. The Cell-Theory.—All organisms have a cellular structure and a cellular origin.

4. A protoplasmic basis now being laid. The "germ-plasm" more important than the egg-cell. All to be interpreted in terms of protoplasmic changes.

5. The contrast between Protozoa and Metazoa.—The making of a "body" as distinct from reproductive cells.

6. General origin of the sex-cells, indefinite in sponges, variable in cœlenterates, generally from the mesoderm in higher animals.

7. Early separation of the reproductive cells to be seen in a minority of cases.

8. The contrast between somatic and reproductive cells, and the continuity of the latter; Owen, Haeckel, Rauber, Brooks, Jäger, Galton, Nussbaum, Weismann.

9. Weismann's theory of the continuity of the germ-*plasm* (a specific *nuclear* matter), as opposed to continuity by a lineage of undifferentiated germ-*cells*, which is known to occur only in a minority of organisms.

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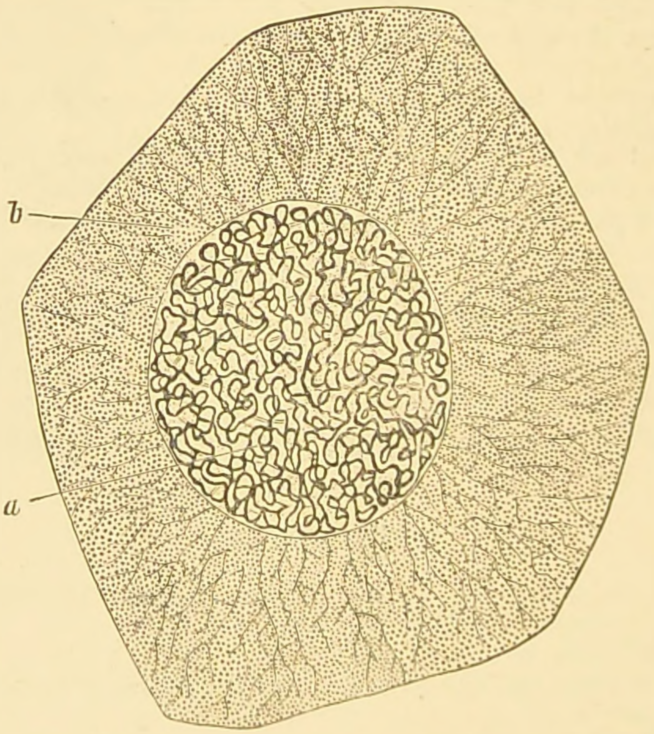
CHAPTER VIII.

The Egg-Cell or Ovum.

In the preceding chapter we sketched the history of the "ovum-theory," which expresses the now familiar fact that every organism, reproduced in the ordinary way, develops from a fertilised egg-cell. The exceptions are the unicellular plants and animals, all forms of asexual reproduction, and the special



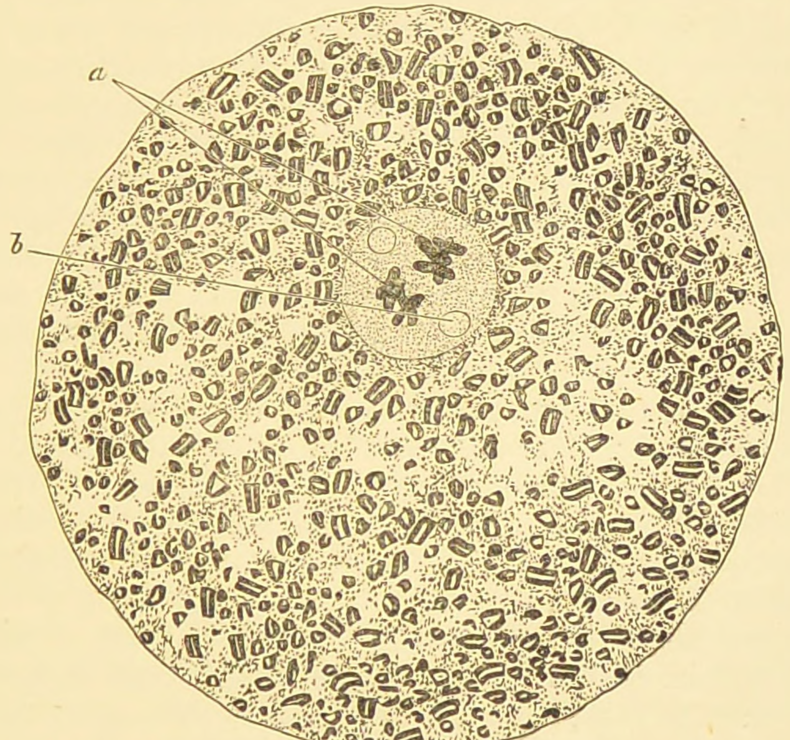
Animal Cell, showing the chromatin elements of nucleus (*a*) in a long coil, and the protoplasmic network (*b*) round about.—From Carnoy.

case of parthenogenesis (where the egg-cell is not fertilised). It is now necessary to attend more carefully to the essential characters and history of this "primordium commune," the starting-point of the individual life.

§ 1. *Structure of the Ovum.*—The ovum presents all the

essential features of any other animal cell. There is the cell-substance, consisting in part of genuine living matter or protoplasm; and there is the nucleus, or "germinal vesicle," which plays such an important part in the ripening, fertilising, and subsequent division of the cell.

Besides the living matter, there are simpler substances, especially in many cases a reserve capital of yolk nutriment for the future embryo. The modern masters of microscopic technique have detected many marvels in the egg-cell, into



Ovum of a Threadworm (*Ascaris*), showing (*a*) the chromatin elements of the nucleus, and the appearance of the surrounding yolk.—From Carnoy.

which we cannot at present enter, but it is important to recognise clearly that although the ovum is in a sense simple, being a single cell, it is not structureless like white of egg. About details there is great diversity of opinion, but all are agreed that the ovum has "organisation."

When Purkinje, in 1825, discovered the nucleus of the fowl's egg, he probably had little idea that the minute "vesicle" to which he directed the attention of investigators was in reality an intricate microcosm. Little more than ten years

elapsed before R. Wagner began to complicate matters by the discovery of the nucleolus or germinal "spot" within the "vesicle." We now know that the nucleus has not only a very complex structure, but in a sense a strange internal life of its own.

The nucleus, when quiescent, often lies in a little nest or chamber within the cell-substance, and is limited from the latter by a more or less distinct nuclear membrane, which disappears as the period of activity begins. Inside this membrane, it is often possible to distinguish one or more of the aforesaid nucleoli, lying in a more fluid material often called the "nuclear sap." About these nucleoli and bodies more or less like them, about the reasons for their variable number and form, very little that is certain can be said. Much more important is the most conspicuous constituent of the nucleus, a system of strands, coils, or loops, which stain deeply with various dyes, and are therefore known as the chromatin elements. In contrast thereto, the less stainable but perhaps equally essential constituents of the nucleus are distinguished as achromatin.

The chromatin elements in the resting nucleus are oftenest arranged in a manifold coil, like a loosened ball of twine, while in other cases they appear rather as a living network. Whether the coil be continuous, as Van Beneden and others describe, or interrupted, as Boveri and others maintain, is subsidiary to the more striking fact, that in the state of activity the number and disposition of the dislocated or loosened parts of the coil remain definite and orderly, and that their behaviour is so like that of minute independent individualities that any rough-and-ready account of the mechanics of cell division must at once be ruled out of court. It is within the chromatin substance too that the germ-plasm, on which Weismann and others have so much insisted, is believed to have its seat. There can be no doubt that the nucleus is a very important factor in the life of the cell. A non-nucleated fragment cut from a Protozoon may show irritability and contractibility, but it cannot feed, and soon dies. Boveri and Delage have shown in sea-urchins, &c., that an ovum-fragment without a nucleus may be fertilised and may develop into a larva, so that it seems as if the sperm-nucleus may in certain cases suffice, but no instance is known of development without any nucleus.

§ 2. *Growth of the Ovum.*—When the ovum is very young,

it very frequently presents the features of an amœboid cell. In some cases this phase persists for a longer time, as in the ovum of hydra, which in all essentials is comparable to an amœba. Even in the simplest animals, however, the amœboid phase constantly shows a tendency to pass into greater quiescence, to become in fact more or less encysted. So is it with ova, which though at first often resembling various forms of amœboid cells, tend more or less quickly to pass into the encysted phase. The protoplasm no longer flows out in irregular ever-changing processes, but is gathered up into a sphere, rounded off, and surrounded by a more or less definite envelope. This transition from a state of relative equilibrium between activity and passivity, to one in which passivity undoubtedly preponderates, is associated with an increase of nutriment and reserve-products. The ovum feeds, becomes heavy with stored capital, becomes less active, and more encysted in consequence.

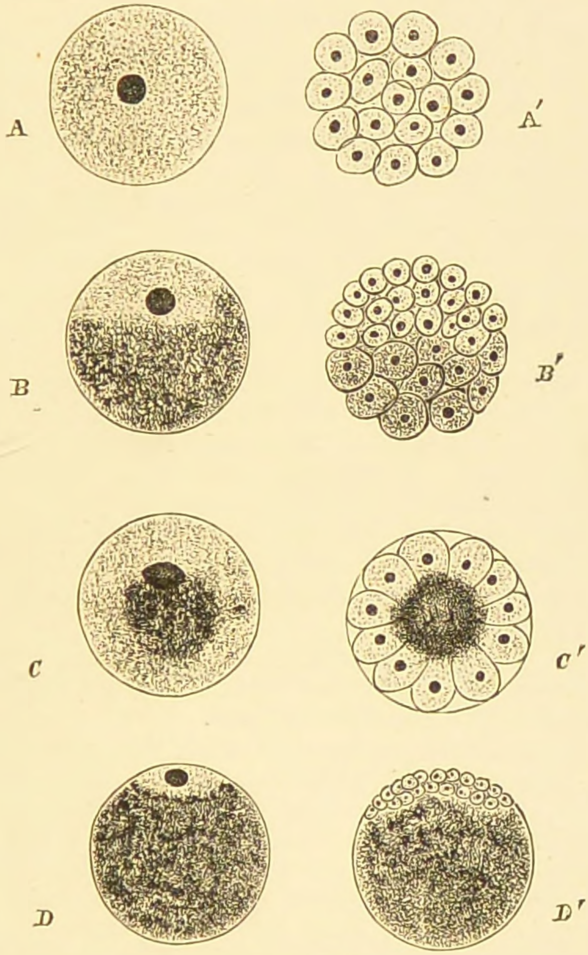
§ 3. *Yolk.*—The essential part of an egg-cell is always small, though even in this there are great differences. The nucleus, for instance, in the large eggs of amphibians, reptiles, and birds, may be detected with the unaided eye; while in other cases, such as sponges, the entire ovum is very minute. Yet every one knows that eggs vary enormously in size. The egg of a skate is very much larger than the egg of a salmon; and the egg-shell of the extinct giant bird of Madagascar (*Æpyornis*) is big enough to hold the contents of one hundred and fifty hens' eggs. Similarly the contrast between the eggs of ostrich and humming-bird is, as one would expect, extremely striking. Yet the eggs of whales are "not larger than fern-seed," and the same is true for most mammals, except the very lowest. The differences in size, when very striking, are due not so much to any marked disproportion in the essential parts of the ova, but to certain extrinsic additions. The most important of these is the yolk, which serves as nutritive capital for the embryo or young animal. Besides the yolk, we have also to take into account the frequent pigment, so familiar in frog spawn, the albumen well seen in the white of birds' eggs, various forms of protective and attaching viscid material, and, lastly, more or less elaborate egg envelopes or shells. The most important, however, is the yolk, and in regard to its origin and disposition a little must be said.

The egg has its nutritive capital increased in three different

ways:—(*a*) Very generally it feeds on the nutritive substances in the general lymph or vascular fluid of body. (*b*) At the same time, or in another case, it avails itself of the *débris* of surrounding cells. In many instances, *e.g.*, in the minute ovary of hydra, in the ovary of *Tubularia*, or in the ovarian tubes of insects, the ovum is but the surviving competitor among a crowd of surrounding cells, which to start with were all potential ova. This is an often forgotten chapter in the struggle for existence,—the struggle between germ-cells. There is a struggle between potential ova; there is also enormous elimination among the spermatozoa, even after they come to close quarters with the ovum. Many are almost successful, but in most cases only one fertilises, *i.e.*, survives. And even after the eggs begin to develop there is often elimination apart from enemies, thus it is stated that only about a third of the eggs of the New Zealand "lizard" (*Sphenodon* or *Hatteria*) ever hatch. (*c*) In the third place, and this is the rarest form, the egg-cell acquires a store of food-material from a special yolk gland, as in many of the lower "worms."

The yolk, gained in one of the ways mentioned above, is more or less readily distinguished from what is often called the formative protoplasm. Out of the latter the embryo is built up, while the yolk has for the most part only a secondary and nutritive *rôle*. We cannot enter here into a discussion of the difficult embryological question as to the extent in which the yolk ever shares in directly contributing to embryonic structures. The possibility of distinguishing between formative protoplasm and the nutritive material, depends on the quantity of the latter that is present, and on the way in which it is disposed. (*a*) When there is not much of it, as in the small ova of mammals and many invertebrates, the yolk material is diffusely distributed. Then the ovum undergoes complete segmentation. (*b*) In the frog's ovum, on the other hand, there is a large proportion of yolk, which has especially accumulated in the lower hemisphere of the cell, while the darker half includes the truly formative protoplasm. In this case too the egg divides as a whole, but the divisions go on much more rapidly in the upper hemisphere, and it is there that the embryo is really formed. (*c*) A distinct mode of yolk arrangement occurs in arthropods (crustaceans, insects, &c.), where the centre, not a pole, of the ovum is occupied by

the nutritive material. In this case the formative protoplasm divides round about the nutrient core. (*d*) In the majority of fishes, in reptiles, and in birds, the eggs show a much more marked polar accumulation of yolk. On the top of a large mass of nutritive material, the specifically lighter formative protoplasm lies like a tiny drop, and in those cases the division



The relation between the disposition of the yolk and the mode of segmentation:—A, diffuse yolk, *e.g.*, sponge; B, polar, *e.g.*, frog; C, central yolk, *e.g.*, crayfish; D, predominant, *e.g.*, bird:—A', Total and equal segmentation; B', total and unequal; C', partial and peripheral; D', partial and discoidal segmentation.

of the ovum is very partial,—that is, it is mainly restricted to the upper formative region. It is thus to be noted that the quantity of yolk present, and its diffuse, polar, or central arrangement, are associated with striking differences in the degree and symmetry of the segmentation.

§ 4. *Composite Ova.*—We have emphasised the fact that the ovum must be regarded as a single cell. To this a definite but pedantic objection has been raised. In some parasitic flat-worms there occur what have been called compound ova. A minute single cell arises, as usual, in the ovary, but in the course of its somewhat intricate history this becomes associated with several nutrient cells derived from the yolk-gland. These surround the original ovum, so that the whole now consists of several cells. But it must be noticed that only the central cell—the ovum proper—is fertilised, and that it contains all the formative protoplasm. Those that surround it are wholly nutritive; they eventually break up, and are absorbed.

In other cases, especially in insects, the ovum grows rich at the expense of neighbouring cells, which are sacrificed to its nutritive equipment. But it is evident enough that a cell remains a cell, however many of its neighbours it may happen to absorb.

§ 5. *Egg Envelopes.*—The ovum starts as a naked cell, but generally becomes furnished with ensheathing envelopes. The exact history of the egg-membranes and sheaths is a very complex matter. Only the most general facts can here be stated. The envelopes may be derived (*a*) from the ovum itself, (*b*) from surrounding cells, (*c*) from the secretion of special glands.

(*a*) Just as a protozoon often exhibits distinct outer and inner zones, distinguished by minor physical and chemical peculiarities, so it is with the ovum. What are called yolk or vitelline membranes are generally produced by the ovum itself. Furthermore, the outer protoplasm often forms a distinct firm zone, known as the *Zona pellucida*. This may be traversed by fine radiating pores establishing nutritive communication with the exterior, and is then known as the *Zona radiata*. A special aperture or *micropyle* is sometimes present, through which the sperm enters, or nutritive supply is sustained.

(*b*) The ovum, in its young stages, is very frequently seen surrounded by a circle of small cells, which form what is called a follicle. These may produce a membrane or a glairy investment.

(*c*) As the ovum ripens, and passes from the ovary into the duct, it often becomes surrounded by gelatinous, horny, limy, and other investments. In most cases, it necessarily follows that the egg has first been fertilised. The investments are usually referable to the activity of the walls of the oviduct or uterus, though sometimes there are special shell-glands, and the like. The chitinous cases of some insect ova, the horny mermaids' purses of many gristly fishes, the more or less limy egg-envelopes of reptiles, the firm limy egg-shells of birds, so often stained with pigments, afford good illustrations of these secondary investments. Quite distinct are cocoons, such as those of earthworm and leech, which surround several eggs, and are produced from the skin of the animal.

It may here be noted that the rather puzzling bodies known as "wind-eggs," or more naïvely as cock's eggs, and regarded by some as the products of immature or exhausted females, are most probably not eggs at all, but simply masses of albumen formed in the oviduct and coated with a shell. (Raspail, "Bull. Soc. Zool. France," xxiii., 1898, pp. 94-97.)

§ 6. *Birds' Eggs.*—The student may be fitly directed to the egg of the fowl, or of some other bird, for a convenient concrete illustration of many facts. There he will see the great mass of

yolk, of two kinds, yellow and white, and on the top of this the minute area of formative protoplasm. It was on this, as it gradually revealed the cloudy outlines of the embryo chick, that the Greeks looked with naïve unaided eyes. Here it was that Aldrovandus, Harvey, Malpighi, Haller, and the early embryologists, with clear vision, saw almost as much as their appliances would permit. It was this which, in its primitive simplicity, impressed Wolff with the reality of epigenesis; and it is this that the observers of to-day look down upon through their embryoscopes, or cut sections of with their microtomes. Then round about all is the secondary investment of "white of egg" or albumen; round this a shell membrane, between the two layers of which the little air-chamber is formed at one end; and finally, the hard but porous limy shell. Mr Irvine, of Granton, has shown that fowls kept with access to no carbonate of lime, but only to other salts of lime, can still form a normal shell. This still consists of carbonate of lime, and is as firm as usual, demonstrating, like the same investigator's experiments on crabs, that animals possess no little power of changing one salt of lime into another. Then, in the eggs of other birds, the import of the seven or more pigments which produce the marvellous variety and beauty comes into question. Sorby has shown that they are related to the pigments of blood and bile; but what they exactly mean no one yet knows. Wider still, the problem arises of how this coloration is so often protective. Or again, there is the curious fact that the size of the egg is often much out of proportion to the size of the bird, and the question arises as to how far this can be interpreted as the result of the more or less anabolic and sluggish constitution.

§ 7. *Chemistry of the Egg.*—Every one knows that the eggs of birds form highly nutritious diet. As the egg contains nourishment for the young bird for a considerable time, it must, like milk, contain all the essentials of food. The results of a recent analysis of the fowl's egg may be taken as a sample.

The germinal or formative disc consists chiefly of albuminoid bodies, apparently of the globulin group, plus smaller quantities of lecithin and the like. The subtle protoplasm itself, it need hardly be said, defies analysis.

In the yolk there are firm fats (tripalmitin, probably plus a little stearine), and a fluid oil or glyceride. Fatty acids develop during hatching. A relatively large quantity of lime is present, probably, for the most part, as calcium albuminate. In the white of egg there are true albumins, also globulins, and the quantity of peptones increases with the age of the egg.

During development the embryo becomes richer in mineral matters, fat, and albumen, and the dry substance of the whole contents of the egg diminishes considerably.

The yolk of many different kinds of ova has been analysed, and the component substances distinguished as *Ichthin* (fishes), *Emydin* (tortoise), and the like. More important were the discoveries of *cholesterin*, *vitellin*, *nuclein*, *lecithin*, and, in association with the latter, *neurin*. As we cannot here enter into the physiological import of such substances, it is enough to say that the nutritive material in ova usually consists of a mixture of complex, unstable, and highly nutritive substances.

§ 8. *Maturation of the Ovum.*—When the egg-cell has attained its mature size, a more or less enigmatical occurrence takes place. The nucleus, hitherto generally central, moves to the pole, alters considerably in its structure, and divides. A minute cell, with half of the nucleus, and a small amount of protoplasm, is given off. Not long after, the nucleus remaining within the ovum repeats the process, and another tiny cell is expelled. This process is known as the extrusion of the polar globules. Of general, and probably of universal occurrence, it has been most satisfactorily studied in invertebrate types. There is considerable diversity as to the exact time at which the extrusion occurs; generally, however, it precedes the entrance of the fertilising sperm. The minute extruded cells never have any history, though they occasionally linger for a considerable time on the outskirts of the ovum. As an exception, they have been seen themselves to divide, and, with equal rarity, a misguided spermatozoon has been observed to penetrate them. Usually, however, they simply dwindle away. The remaining female nucleus of the ovum is now ready to unite with the male nucleus of the spermatozoon. At this point, awaiting the essential moment of fertilisation, we shall for the present leave it.

Weismann, assisted by C. Ischikawa, has demonstrated an exceedingly interesting fact in regard to polar globule extrusion in parthenogenetic ova. Instead of the two polar globules which are usually extruded, parthenogenetic ova were shown to form only one. This was demonstrated in a variety of cases,—in water-fleas (daphnids and ostracods) and rotifers,—and is believed to be a general fact. Blochmann, who has been successful in demonstrating polar globules in several orders of insects, has also observed that in the parthenogenetic ova of the plant-louse or aphis, only one polar globule is formed, while in other non-parthenogenetic aphid eggs, which only develop

after fertilisation, two occur as usual. To these facts we must afterwards recur in connection with parthenogenesis.

What must be emphasised, however, is this:—the nuclei of the mature ovum and spermatozoon contain half the number of nuclear rods or chromosomes characteristic of the body-cells of the animal in question. In their early immature stages they contain the normal number. Therefore a reduction—a halving—of the number must take place during the process of maturation. The same is true in plants.

Similarly, before the nuclear fusion in two conjugating individuals of the sun-animalcule (*Actinophrys sol*), there is, as Schaudinn has shown, a "reduction-division," half of each nucleus being got rid of, and there are several other phenomena in Protozoa which appear to be analogous to the maturation-processes in the ova of Metazoa.

§ 9. *Theories of the Polar Globules.*—The polar globules appear to have been first observed in 1848 by Fr. Müller and Lovén, but it is only within recent years that much has been made of them. Thanks to the masterly researches of Bütschli and Hertwig, Giard, Fol, and others, it became possible to interpret the extrusion as a case of cell-division or budding. More recently, Van Beneden, whose monograph on the ovum of the threadworm (*Ascaris*) will remain one of the classics in this department of research, has raised a protest against regarding the extrusion as a normal cell-division. The details of the process, as interpreted by him, seemed to mark out the extrusion as something unique. Most authorities, however, adhere to the older view, that the process is essentially one of normal cell-division.

As to the meaning of the process, the chief opinions, only a mere outline of which can be given, are three, not including a number of suggestions according to which the extrusion of the globules is a kind of "excretion" of the ovum, or a "rejuvenescence" of the nucleus.

(*a*) According to some, the egg-cell is in a sense hermaphrodite, and the polar-globule formation is an extrusion of the male element. Balfour expressed his view in somewhat teleological language:—"I would suggest that in the formation of the polar cells, part of the constituents of the germinal vesicle, which are requisite for its functions as a complete and independent nucleus, is removed to make room for the supply of the necessary parts to it again by the spermatic nucleus. . . . I will venture to add the further suggestion, that the function of forming polar cells has been acquired by the ovum for the express purpose of preventing parthenogenesis." To this it must now be pointed out, that so far as one polar globule is concerned, extrusion does not prevent parthenogenesis. This view seems, according to Brooks, to have been first advanced by M'Crady. It has been most carefully elaborated by Minot. According to Minot, "in the cells proper, both sexes are potentially present; to produce sexual elements the cell divides into its parts; in the case of the egg-cell, the male polar globules are cast off, leaving the female ovum." In parthenogenetic ova, he supposes that enough male element is retained, since only

one polar globule appears to be formed. Van Beneden, whose opinion is entitled to great weight, also inclines to regard the polar globules as male extrusions.

Sabatier distinguishes, besides true polar globules, other extrusions, and believes the eliminated parts to be male elements. His views are connected with an elaborate theory of polarities, according to which, for instance, the peripheral extrusions are male, while central cores (in the development of sperms) are female residues.

(*b*) A very different view—morphological rather than physiological—has been maintained by Giard (1876), Mark (1881), Bütschli, Whitman, and others, that the polar bodies are equivalent to ova. The formation of polar globules is an atavistic reminiscence of primitive parthenogenesis. Just as the mother sperm-cell or spermatogonium, which corresponds in the male to the ovum in the female, divides up into what form spermatozoa, so the ovum retains a slight power of division. In short, the polar globules are "abortive ova."

(*c*) According to Weismann, Hertwig, and others, the gist of the matter may be expressed by the term "reducing-division." In different species the cells of the body are characterised by the possession of a definite number of chromatin elements. Thus, in one variety of the round-worm of the horse there are four, in man there are two hundred. In the maturation of ovum and spermatozoon the number is reduced preparatory to fertilisation, so that the fertilised ovum contains the normal quota, and not double that as would be the case were there no reduction. The period and the details of the reduction seem to differ greatly, but the general fact stands out clearly that maturation implies a reduction of the number of chromosomes in the ultimate germ-cells to one-half the number characteristic of the somatic cells of the species. The reduction phenomena occur in plants as well as in animals, but the details remain somewhat uncertain. In the higher plants the reduced number is seen in all the cells of the sexual or gametophyte generation, beginning with the asexual mother-spore-cells from which this generation arises.

SUMMARY.

1. The ovum presents all the essential features of a cell—cytoplasm, nucleoplasm, etc.

2. The ovum often passes from an amœboid to an encysted phase, with increase of nutrition and size.

3. The yolk is derived from the vascular fluid, or surrounding cells, or special glands, and is present in varying quantity and disposition. If little, it is diffuse; if much, it is polar or central; and the different modes of egg-division are associated with this.

4. In some cases the ovum is surrounded by a number of nutritive cells (composite ova), and often becomes what it is by preying upon its neighbours. This hardly affects its unicellular character.

5. Egg-envelopes are produced from the ovum itself (*e.g.*, vitelline membrane), or from surrounding cells (follicular sheath), or from special glands (the outside shell).

6. Bird's egg noted as a concrete illustration of facts and problems.

7. The egg, so far as its nutritive material is concerned, includes a mixture of complex, unstable, highly nutritive substances.

8. The maturation of the ovum is usually associated with a double cell-division, known as the extrusion of polar globules. In parthenogenetic ova only one occurs, with rare exceptions.

9. These polar globules have been interpreted variously:—(*a*) As extrusions of male elements; or (*b*) as abortive ova; but (*c*) the whole process implies a reduction of nuclear rods or chromosomes, preparatory to fertilisation.

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CHAPTER IX.

THE MALE-CELL OR SPERMATOZOON.

§ 1. *The General Contrast between Ovum and Spermatozoon.* —Just as the ovum, large, well nourished, and passive, is as such a cellular expression of female characteristics, so the smaller size, less nutritive habit, and predominant activities of the spermatozoa illustrate the qualities of maleness. As the ovum is usually one of the largest, the sperm is one of the smallest of cells, sometimes only $\frac{1}{100,000}$th of the size of the ovum, which is often microscopic. The yolk or food-capital, and encysting membranes, which are often so prominent in the former, are as conspicuously absent in the latter. The contrast, though less accented, is still quite discernible in plants. In fact, the two kinds of cells are just as widely opposed in their general features, as they are fundamentally complementary in their history. Before this opposition and complementariness can be fully understood, however, we must briefly sum up the characters and history of the male elements.

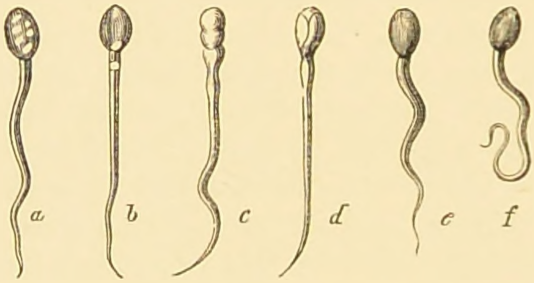
§ 2. *History of Discovery.*—In 1677, one of Leeuwenhoek's students, Hamm by name, called his master's attention to the minute elements actively moving in the male fluid. Leeuwenhoek, who some years previously for the first time observed what we now know as unicellular organisms, was at once impressed by the import of the marvellously active male units. Almost too much impressed, in fact, for he interpreted them as minute preformed germs, which only required to be nourished by the ovum to unfold into embryos. Thus the unfortunate aberration, already noted as the doctrine of the animalculists, had its origin. For long no progress whatever was made; some naturalists, like Vallisneri, depreciating the import of the sperms altogether, and regarding them as worms which hindered the coagulation of the seminal fluid; others going to the opposite extreme, and regarding them as nests of germs. Thus Haller at first considered them to be what Leeuwenhoek had suggested, but afterwards admitted them merely as *nativi hospites seminis.* In 1835, even Von Baer was inclined to interpret them as minute parasites peculiar to the male fluid; and if the curious student will turn up the article *Entozoa* in Todd's "Cyclopædia of Anatomy and Physiology," of about the same date, he will find that the veteran Owen includes the spermatozoa under that strange

heading. The very name spermatozoon recalls the view which so long prevailed.

In 1837, R. Wagner emphasised their constancy in all the sexually mature males which he examined, and their absence in infertile male hybrids. Von Siebold demonstrated their presence in many of the lower animals; and lastly, in 1841, Kölliker made one of his many important contributions to biology, in proving that the sperms had a cellular origin in the testes.

§ 3. *Structure of the Sperm.*—The sperm, then, is a cell. Though some, such as Kölliker, have inclined to regard it rather as a nucleus, its truly cellular character has been proved beyond dispute. As in the ovum, there is cell-substance and nucleus, with this marked difference, that the cell-substance is generally reduced to a minimum.

The sperm is almost always, moreover, a cell of a very definite type or phase. It is like one of the highly motile



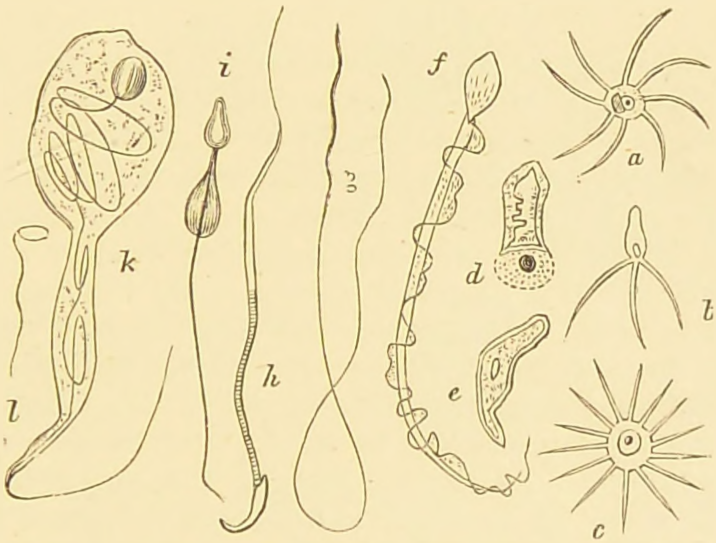
"Spermatic Animalculi" of the Rabbit and the Dog.
—From Buffon, after Leeuwenhoek.

Protozoa, like a flagellate infusorian. Usually it consists of a minute "head," consisting almost entirely of nucleus, and of a long contractile tail, which, working behind like a screw, propels the essential "head" through the water or along the ducts. Between the head and the tail there is an important middle portion, which many observers agree in regarding as the bearer of the centrosome—a now well-known component of a typical animal cell.

Occasionally there is a departure from the usual flagellate type. Thus in the threadworm *Ascaris*, the sperm has a blunt pear-shaped form, and exhibits slight amœboid movements. In some crustaceans and other arthropods, the cell is even more quiescent, and may exhibit curious forms, such as that figured for the crayfish. The relatively dormant activity may however wake up, and the sperm exhibit active amœboid movements. Zacharias has made some interesting experiments, showing the

modifiability of sperms under reagents; thus, in a little crustacean (*Polyphemus pediculus*), he first caused the cylindrical sperm to form amœboid processes, and afterwards to replace these by what were to all intents and purposes cilia. This is entirely congruent with other experiments and observations on the passage of cells from one phase of the cell-cycle to another.

F. Silvestri records the interesting case of the millipede *Pachyiulus communis* in which the spermatozoon is immobile and cap-shaped, and is drawn into the ovum by a pseudopodium emitted by the latter through the micropyle. In other words, the ovum here plays the active rôle, and the spermatozoon is passive. ("Atti Acc. Lincei (Rend.)," vii., 1898, pp 129-133, 5 figs.)



Spermatozoa of crayfish (*a*), lobster (*b*), crab (*c*), ascarid (*d*), water-flea—Moina (*e*), man (*f*), ray (*g*), rat (*h*), guinea-pig (*i*), a beetle—immature stage (*k*), sponge (*l*). (Not drawn to scale.)

The progress of microscopic technique has demonstrated many complexities in the sperm as well as in the ovum. For a discussion of some of the more important of these, the reader is referred to the "Encyclopædia Britannica," article *Reproduction*. A few points only need be noticed here. Thus most spermatozoa exhibit not only a head (almost wholly from the nucleus of the mother-cell) and a mobile tail (from the substance of the mother-cell), but a median portion connecting these. The tail is not unfrequently, as in salamander and man, furnished with a very delicate undulating or vibratile band, and often shows, as in birds, an axial filament, which like many other contractile structures is distinctly fibrillated. In a few cases, as in the threadworm, the sperm is not left without any nutritive capital, but furnished with this in the form of a cap, which falls off before the essential moment of fertilisation arrives. It is very generally admitted

that the head consists almost wholly of chromatin, and that the tail is mainly cytoplasmic, *i.e.*, formed of cell-substance. The middle part connecting head and tail is believed by many to be formed by the centrosomes, which play some part in the division of the egg. In the non-flowering plants the male-cells or antherozoids often bear a close resemblance to those of animals; in the flowering plants the male-elements are the reproductive nuclei which issue from the pollen-tube; but the discoveries of Hirasé and Ikeno have shown that even in flowering plants, namely in Cycads, there are motile spermatozoa. It is of interest to notice that a dimorphism of spermatozoa has been recorded in various cases, *e.g.*, by Auerbach for water-beetles, and even in man by Bardeleben. As has been already noted, there is sometimes, as in Rotifers, a dimorphism of ova, and it is probable that we have here again an illustration of the fundamental variational alternatives,—between relatively katabolic and relatively anabolic phases. Apart from this dimorphism, it should be noted that in the testis of many higher animals, there seems to be, as in the ovary, a division of labour between germ-cells proper and nutritive cells auxiliary to these.

§ 4. *Physiology of the Spermatozoon.*—A few facts in regard to the physiology of the sperm demand notice. (*a*) It is specialised as a highly active cell; its minimal size, the usual absence of any encumbering nutritive material, the contractility of the tail, and the general shape, all fit it for characteristic mobility. More than one histologist has likened it to a free muscle-cell, or to a flagellate monad. (*b*) Furthermore, the sperm has very considerable power of persistent vitality. Not only does it often remain long unexpelled in the male animal, without losing its functions, but it may retain its fertilising power after remaining for weeks, or even months, in the female organism. In the earthworm, the spermatozoa pass from one worm to another, not directly to the ova nor to female ducts, but to be stored up in special reservoirs or spermathecæ. So it is with many animals. The spermatozoa received by the queen bee during her single impregnation, are for a considerable period—even for three years—used in fertilising successive sets of worker and queen ova. Quite unique, however, is the case of one of Sir John Lubbock's queen ants, which laid fertile eggs thirteen years after the last sexual union with a male. The spermatozoa had apparently persisted all that time. Hensen cites the facts that a hen will lay fertilised eggs eighteen days after the removal of the cock, and that in bats, spermatozoa may remain alive a whole winter in the uterus of the female. In most European bats, indeed, sexual union occurs in autumn, but the sperms are simply stored in the uterus, for ovulation and fertilisation do not take place till

spring. In exceptional cases, especially in young forms which were not mature in autumn, pairing occurs in spring. An exactly parallel condition is known in some snakes. Thus Rollinat notes in regard to *Tropidonotus viperinus* that mature females are inseminated in the autumn previous to the egg-laying (in June or July), but in females laying for the first time, copulation probably occurs in early spring ("Bull. Soc. Zool. France," xxiii., 1898, pp. 59-63). (*c*) Remarkable too, and again suggestive of monads, is the power the sperms have of resisting great deviations from the normal temperature. The presence of acids has usually a paralysing influence, but alkaline solutions have, on the whole, the opposite result.

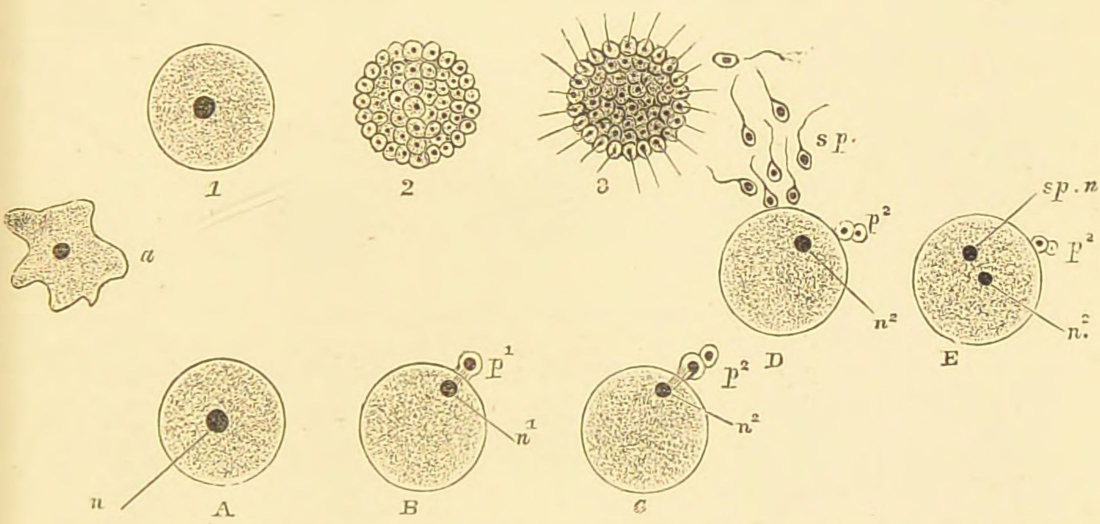
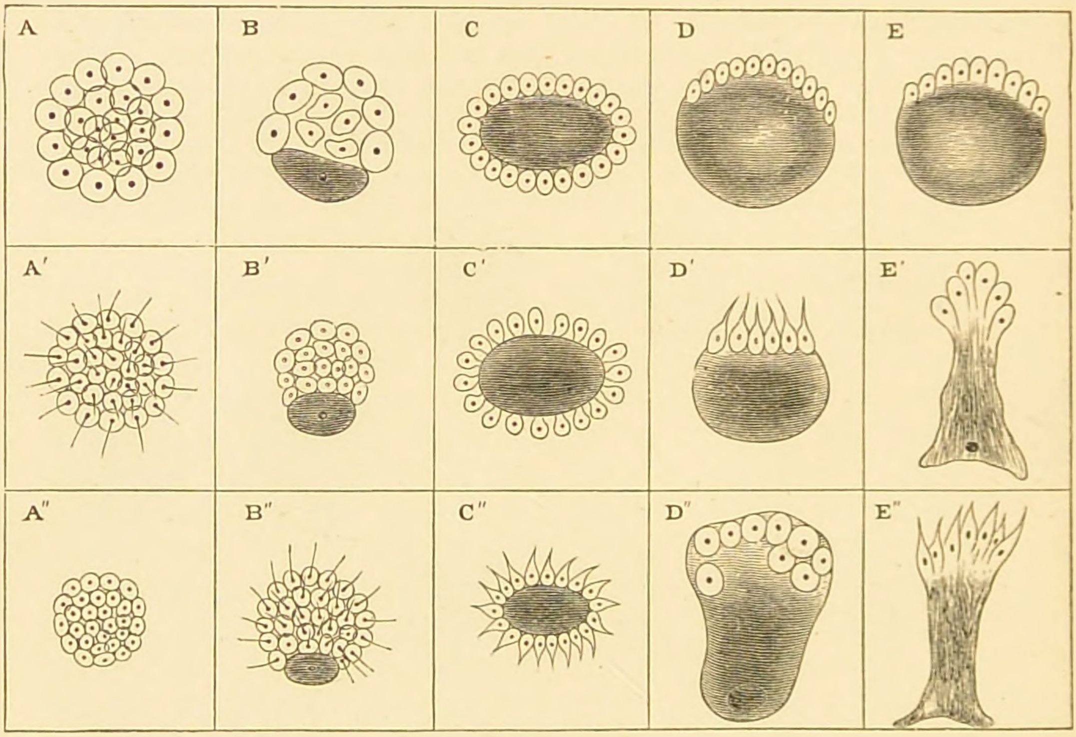


Diagram of the Development of Spermatozoa (upper line), of the Maturation and Fertilisation of the Ovum (lower line).
a, an amœboid sex-cell; A, ovum, with germinal vesicle, *n*; B, ovum extruding first polar body, p^1; C, extrusion of second polar body, p^2, nucleus n^2, now reduced. 1, a mother-sperm-cell, dividing (2, 3) into immature and mature spermatozoa (*sp.*).
D, the entrance of a spermatozoon; E, the male and female nuclei *sp. n* and n^2 approach one another.

§ 5. *Origin of the Sperms.*—For the last twenty years the development of spermatozoa has been the subject of almost continuous research and controversy, and the all too-abundant nomenclature affords a suggestive index to the confusion out of which the subject is now emerging. In a general way, the process is simply that of the varied segmentation of a mother-sperm-cell, and the occurrence of a series of preparatory stages before the sperm is finally matured. In detail, however, there are many variations, and these are described in a maze of often tautologous and ambiguous terms, such as spermatogonium,

spermatoblast, spermatospore, spermatogemma, spermatomere, spermosphere, and a dozen more.

One of the most defensible set of terms is that used by Voigt after Semper, and also by Von la Valette St George. The sperm or spermatozoon is differentiated from an immature cell or spermatide, this is modified from or descended from a spermatocyte, the spermatocytes result from the division of the mother-sperm-cell or spermatogonium, and this finally is a modified form or a descendant of the primitive sex-cell or male ovule.



Comparison of Spermatogenesis and Ovum Segmentation.

EXPLANATION.—The first line, A–E, exhibits types of ovum segmentation:—A, regular morula; B, unequal segmentation, *e.g.*, in some Molluscs; C, centrolecithal or peripheral type, *e.g.*, in a shrimp Peneus; D, discoidal segmentation; E, the same, with the cells less markedly defined off from the yolk.

In the next two lines various types of spermatogenesis are collated with the above to illustrate the parallelism:—A′ and A″, morula type, as in Sponge, Turbellarian, Spider, &c.; B′ and B″, where the division is unequal, and one large nutritive cell is seen (Plagiostome fishes, after Von la Valette St George); C′ and C″, after Blomfield, Jensen, &c., showing central cytophoral or blastophoral nutritive portion; D′ and D″, sperm-blastoderm, with a few formative cells on large nutritive blastophore, after Gilson, &c.; E′ and E″, the same, with the sperm cells less definitely separated off, after Von Ebner and his followers.

Difficulties become thick, however, when we inquire into the division of the mother-sperm-cell or spermatogonium, and it is here that the observations of recognised authorities so much disagree. Accepting the results of competent observers, we have elsewhere endeavoured to rationalise and unify the conflicting observations, by comparing the different modes of spermatogenesis with the different forms of ovum-segmentation. It has

been already incidentally noticed that the egg-cell may divide wholly and equally, or unequally, or only very partially, or round a central core. Just in the same way the mother-sperm-cells may divide into a uniform ball of cells, or only at one pole, or only at the periphery round a central residue. Balfour and others had hinted at this comparison in the use of terms like sperm-morula; and Hermann had also concluded, "that the division of the male ovule into a series of generations of daughter-cells, is a phenomenon comparable to that exhibited by the ovum in the formation of the blastoderm. . . . It seems then more important to determine exactly the mechanism of division, than to give a particular name to each stage of segmentation."

Although this interpretation of spermatogenesis by collating it with ovum segmentation appears to Minot "a fanciful comparison," in favour of which he is "unable to recognise any evidence," neither the initial homology between the mother-sperm-cell and ovum with which we start, nor the striking parallelism between the modes of division of these homologues, seem thereby even disputed, much less shaken. The widely different conditions in which these two processes occur, and their very different meaning to the organism, are of course obvious.

§ 6. *Further Comparison of Ovum and Sperm.*—It is often said that the sperm is the male cell which corresponds to the ovum. This is only true in a certain sense. In function the two elements are indeed, in a general way, of equal rank, and are obviously complementary. But even in this respect, the two elements, which unite in equal proportions in the essential act of fertilisation, are not exactly sperm and ovum, but (*a*) the head or nucleus of the sperm and (*b*) the female nucleus doubly reduced by the extrusion of two polar globules. The accurate structural resemblance or homology seems to be between oogonium or primitive female germ-cell and spermatogonium or primitive male germ-cell, or between the immature ovarian ovum or oocyte and the spermatocyte.

The parallelism between the reduction of the number of chromosomes in the maturation of the ovum and the similar reduction in the course of spermatogenesis is of great interest and importance. Unfortunately the results of different observers and in regard to different organisms remain perplexingly discrepant. Professor E. B. Wilson gives the following statement with special reference to the case of *Ascaris megalocephala*, the threadworm of the horse:—

"Like the ova, the spermatozoa are descended from primordial germ-cells which by mitotic division give rise to the *spermatogonia* from which the spermatozoa are ultimately formed. Like the oogonia, the spermatogonia continue for a time to divide with the usual (somatic) number of chromosomes, *i.e.*, four in *Ascaris megalocephala bivalens*. Ceasing for a time to divide, they now enlarge considerably to form *spermatocytes*, each of which is morphologically equivalent to an unripe ovarian ovum, or *oocyte*. Each spermatocyte finally divides twice in rapid succession, giving rise first to two daughter-spermatocytes and then to four *spermatids*, each of which is directly converted into a single spermatozoon. The history of the chromatin in these two divisions is exactly parallel to that in the formation of the polar bodies. . . . From each spermatocyte arise four spermatozoa, and each sperm-nucleus receives half the usual number of single chromosomes. The parallel with the egg-reduction is complete."

§ 7. *Chemistry of the Sperm.*—Comparatively little has been done in

regard to the chemistry of the male elements in different animals. The most important observations are those of Miescher, on the milt of salmon. His analysis demonstrated the presence of lecithin, fat, and cholesterin,—also component parts of the ovum. Besides these, after the heads of the spermatozoa have been formed, Miescher detected the abundant presence of a substance which he called *protamine*, a compound of nucleic acid. Albuminoid material, and products of decomposition, such as sarkin and guanin, were demonstrated, according to Hensen, by Picard.

More recently, Kossel has shown that the *protamin* in the salmon's sperms and the analogous *sturin* in those of the sturgeon, act as basic substances forming a salt-like combination with the nuclein substances. ("SB. K. Preuss-Akad. Berlin," 1896, pp. 303-308.)

It is remarkable, however, as Dr T. Gregor Brodie points out ("Science Progress," vii., 1898, pp. 131-149), that the spermatozoa consist of substances which, relatively to proteids, are of simple constitution. "If it be true that hereditary characteristics are transmitted by the chromatin of the reproductive cells, we should have expected a most complex chemical structure for these parts; and it therefore becomes the more striking to note that the most complex protamine as yet obtained, arbacin, is from an animal low in the scale (*Arbacia*, a sea-urchin), and that in the higher vertebrates examined no protamine is present at all."

Zacharias has made a micro-chemical comparison of the male and female elements in Characeæ, mosses, ferns, phanerogams, and amphibians. He finds that the male cells are distinguished by their small or absent nucleoli, and by their rich content of nuclein; while the female elements exhibited a poverty of nuclein, an abundance of albumen, and one or more nucleoli, more or less large in proportion. The male cells have, in relation to their protoplasm, a larger nuclear mass than the female elements.

It is interesting to notice that an analysis of two different kinds of pollen showed a great analogy of composition between these male reproductive cells and those of the salmon and ox.

SUMMARY.

1. The contrast between the elements is that between the sexes. The large, passive, highly-nourished, relatively anabolic ovum; the small, active, relatively katabolic sperm.

2. Hamm's discovery, 1677; Leeuwenhoek's interpretation; the school of animalculists; Kölliker's demonstration of the cellular origin of the sperm, 1841.

3. Structure of the sperm,—nuclear "head" of chromatin, protoplasmic "tail," middle portion. The sperm comparable to a monad or flagellate infusorian, only with less cell-substance. Its occasional degradation into the amœboid phase.

4. Physiology of the sperm; its locomotor energy at a maximum, but yet great power of endurance, like a monad or bacillus.

5. Origin of sperms from the division of a mother-sperm-cell homologous with the ovum. The different modes of "spermatogenesis" may be collated with the different modes of ovum-segmentation.

6. The occurrence in sperm-development of phenomena comparable both structurally and functionally with polar-globule formation.

7. Chemistry of the sperm; resemblance between pollen and spermatozoa.

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CHAPTER X.

Theory of Sex—its Nature and Origin.

Having got so far in our analysis, and before passing to the study of the processes of reproduction, we must add up the results in a general theory of the nature and origin of sex. After this has been done, we shall be in a better position to deal, in Book III., with fertilisation, parthenogenesis, and the like. The number of speculations as to the nature of sex has been well-nigh doubled since Drelincourt, in the last century, brought together two hundred and sixty-two "groundless hypotheses," and since Blumenbach quaintly remarked that nothing was more certain than that Drelincourt's own theory formed the two hundred and sixty-third. Subsequent investigators have, of course, long ago added Blumenbach's "Bildungstrieb" to the list; nor is it claimed that the generalisation we have in our turn offered has yet received "final form," if that phrase indeed be ever permissible in an evolving science, except when applied to what is altogether extinct. This much, however, is distinctly maintained, that future developments of the theory of sex can only differ in degree, not in kind, from that here suggested, inasmuch as the present theory is, for the first time, an expression of the facts in terms which are agreed to be fundamental in biology, those of the anabolism and katabolism of protoplasm.

§ 1. *Suggested Theories.*—According to Rolph,—a fresh and ingenious thinker, removed before attaining his mature strength,—"the less nutritive, and therefore smaller, hungrier, and more mobile organism [cells, he is speaking of] we call the male; the more nutritive, and usually more quiescent organism is the female." He goes on vividly to suggest why "the small starving male cell seeks out the large well-nourished female cell for the purposes of conjugation, to which the latter, the larger and better nourished it is, has on its own motive less inclination."

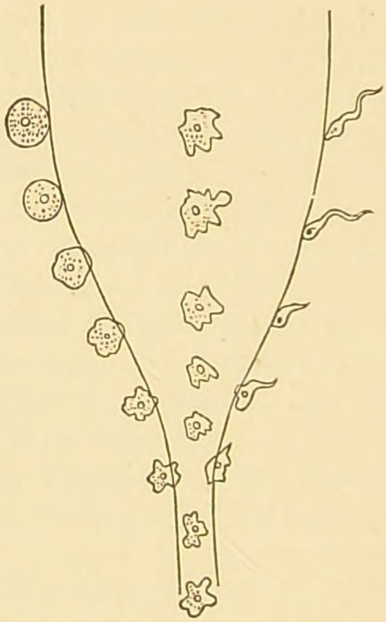
Minot, in his "theory of genoblasts," or sexual elements, ventures little further than regarding male and female as derivatives of primitive hermaphroditism in two opposite directions. "As evolution continued, hermaphroditism was replaced by a new differentiation, in consequence of which the individuals of a species were—some capable of producing ova only, others of producing spermatozoa only. Individuals of the former kind we call females, of the latter males, and they are said to have sex." "At present all we can say is, we do not know why or how sexual individuals are produced." In regard to the sex-elements, we have already noticed his opinion that they are at first "hermaphroditic or asexual," and that both differentiate by the extrusion or separation of the contradictory elements, the ovum getting rid of male polar globules, the sperms leaving behind a female mother-cell-remnant.

Brooks has emphasised rather a different aspect of the question. "A division of physiological labour has arisen during the evolution of life, the functions of the reproductive elements have become specialised in different directions." "The male cell became adapted for storing up gemmules, and, at the same time, gradually lost its unnecessary and useless power to transmit hereditary characteristics." "The males are, as a rule, more variable than the females; the male leads, and the female follows, in the evolution of new races." Brooks does not exactly attack the problem of the nature and origin of sex, but his hypothesis of the greater variability of males is of interest.

To others, again, it seems sufficient to interpret sexual dimorphism as an adaptation evolved in the course of natural selection from variations of which no rationale can be given. As to the adaptive character of sex there can be no doubt, our problem is whether the variations which gave rise to the dimorphism may not be interpreted in terms of the two main alternatives of protoplasmic metabolism.

§ 2. *Nature of Sex as seen in the Sex-Elements—The Cell Cycle.*—As ova and sperms are the characteristic products of female and male organisms, it is reasonable that an interpretation of sex should start at this level. Here, assuredly, the difference between male and female has its fundamental and most concentrated expression. For the bodies, after all, as Weismann has so clearly emphasised, are but appendages to this immortal chain of sex-cells.

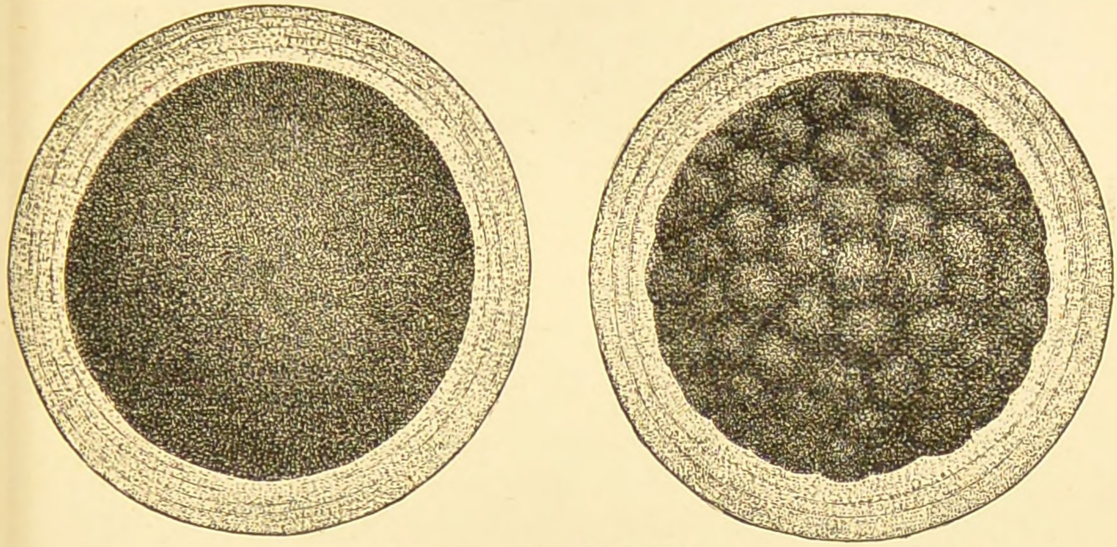
We have already pointed out that the sex-cells are more or less on a level with the Protozoa. If we only knew, they probably differ widely from them in those intricacies of nuclear structure of which we only see the surface; yet as single cells the sex-cells are comparable with the Protozoa. For the moment, let us study those simplest organisms. When we consider an extended series of unicellular forms, amœbæ, foraminifers, sun-animalcules, infusorians, gregarines, and some of the simplest algæ as well, we gradually begin to group these in the mind under three divisions. First there are highly active cells,—infusorians of all sorts; at the opposite extreme there



The divergence of male and female cells from primitive amœboid indifference.

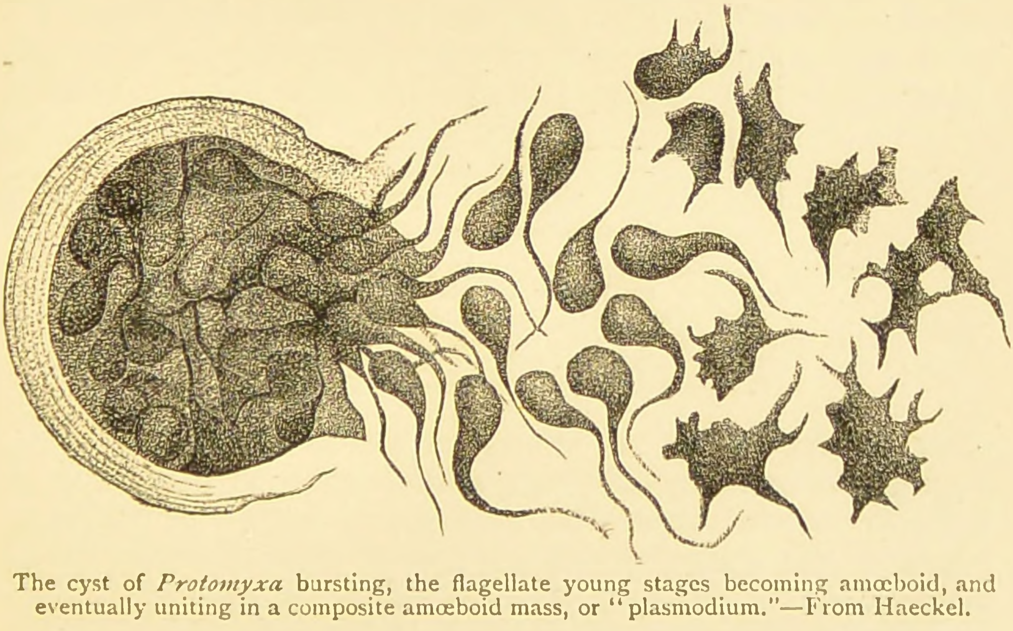
are quiescent forms, in which the life seems to sleep, and locomotion is almost absent,—the gregarines, and some unicellular algæ; and between these there are forms which in a *via media* have effected a sort of compromise between activity and passivity, which are without the cilia of the one or the relative stagnancy of the other, but possess outflowings of their living substance,—the familiar amœboid processes. We may thus reach, almost by inspection, a rough and ready classification of the Protozoa, into active, passive, and amœboid cells,—a classification which, under varying titles, is more or less distinctly recognised by all the authorities on the subject.

But if we go further than casual inspection, and study the life-history of some of the very simplest forms, such as some



The encysted *Protomyxa*, and its division into numerous individuals within the cyst. —From Haeckel.

of the primitive Proteomyxa and Myxomycetes, and follow, for instance, Haeckel's account of the life-cycle in *Protomyxa*, we soon gain new light on our classification. For in these life-



The cyst of *Protomyxa* bursting, the flagellate young stages becoming amœboid, and eventually uniting in a composite amœboid mass, or "plasmodium."—From Haeckel.

histories we find the cells now encysted, now active lashed spores, and again sinking down into the compromise of equilibrium

effected by amœbæ. We are now in a position to recognise that the chapters in the life-history of the simplest forms are, as it were, prophecies of each of the three groups. In other words, the most primitive organisms passed through a cycle of three phases, one of which is accented by each of the three main groups of the Protozoa. And while each main group is characterised by one dominant phase of cell-life,—encysted. amœboid, or flagellate,—there are often transient hints of

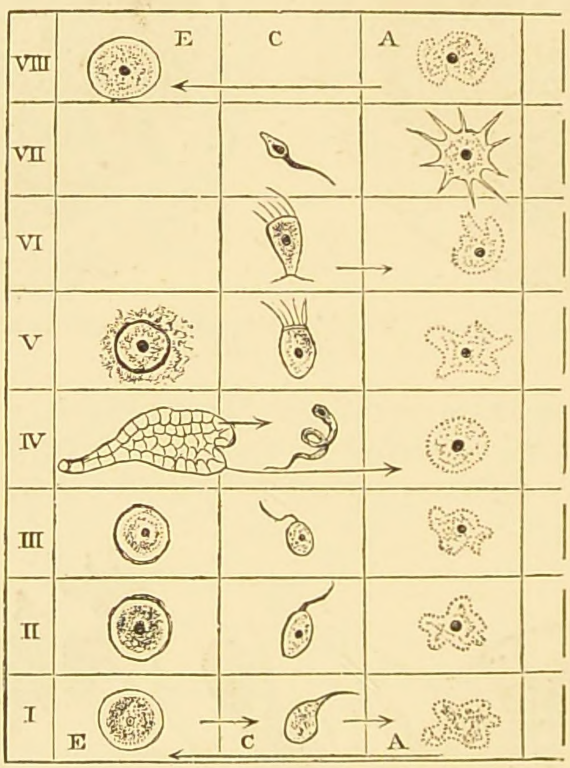


Diagram of the Cell-cycle,—of encysted (E), ciliated (C), and amœboid (A) phases. I., II., III., in Protozoa; IV., ovum and sperm of fern prothallus; V., encysted, ciliated, and amœboid animal cells; VI., ciliated animal cell pathologically becoming amœboid; VII., typical and amœboid sperm; VIII., amœboid and encysted ovum.—From Geddes.

other phases. Thus an infusorian has its encysted chapter, a gregarine its amœboid stage, and a rhizopod may begin as a mobile ciliated spore; for each group, while accenting one phase of the cycle, retains embryonic reminiscences of the others.

We become more convinced that the triple division really means much when we pass from the Protozoa to the cells which compose higher animals. There we find active ciliated cells

in most of the classes, from the ciliated chambers which lash the water through a sponge, to the cells lining the air passages in man; passive encysted cells are illustrated in some forms of connective, fatty, and skeletal tissue; while the white blood corpuscles are obviously comparable to amœbæ. Extended observation here also shows us the cells passing from one phase to another. Our rough classification of the Protozoa is verified in the histology of higher animals, and reappears in the study of their diseases. We are thus at length in a position to say, that however these three phases were brought about, the forms characteristic of them are of such wide occurrence through nature as to justify our restatement of the familiar cell theory in terms of a larger conception, that of the *cell-cycle*. That is to say, from the conception of the cell as a corpuscle of living protoplasm, amœboid, encysted, or ciliated, as the case might be, we come to regard these forms as the predominant phases of a cycle,—primeval, certainly, in the history of the organic world, and largely so even in the individual cell.

A final corroboration of the cell-cycle, and at the same time a *rationale* of it, is obtainable on physiological lines, when we inquire into the protoplasmic processes which lie behind the changes in the form and habit. We have already spoken of the modern physiologist's conception of living matter, or protoplasm, as an exceedingly complex and unstable substance or mixture of substances, undergoing continual chemical change or metabolism. On the one hand, there is a process of construction; the income of nutritive material, at first more or less simple, is worked up by a series of chemical changes till it reaches a climax of complexity and instability. These upbuilding, constructive, synthetic processes are summed up in the term anabolism. But, on the other hand, there is a process of disruption; the complex material breaks down into more and more stable compounds, and finally into waste products. This disruptive, descending series of chemical changes is known as katabolism. Both constructive and disruptive changes occur in manifold series. The same summit may be gained or left by many different paths, but at the same time there is, as it were, a distinct watershed,—any change in the cell must tend to throw the preponderance towards one side or the other. In a certain sense too the processes of income and expenditure must balance, but only to the usual extent, that expenditure must not altogether outrun income, else the cell's capital of

living matter will be lost,—a fate which is often not successfully avoided. The disruptive, or katabolic, or energy-expending set of changes may be obviously greater in one cell than in another, in proportion to the constructive or anabolic processes. Then, we may shortly say that the one cell is relatively more katabolic than the other, or *vice versâ* on the opposite supposition. Just as our expenditure and income should balance at the year's end, but may vastly outstrip each other at particular times, so it is with the cells of the body. Income may for a time preponderate, and we increase in wealth, or similarly, in weight, or in anabolism. Conversely, expenditure may predominate, and business may be prosecuted at a loss; just as we may live on for a while with loss of weight, or with excessive wear and tear. This losing game of life is what we call a katabolic habit, tendency, or diathesis; the converse gaining one being the anabolic habit, tendency, or diathesis. The words anabolic and katabolic are, of course, unfamiliar, and undeniably ugly. Habit and temperament have very vague associations, and tendency sounds metaphysical; diathesis, again, seems no better than the medical equivalent of this. These things the reader must naturally feel; yet the medical man has some definite concrete meaning in his mind when he speaks of gouty or neurotic diathesis, of bilious habit, strumous tendency, or the like. There is more than metaphysical vagueness in his phraseology, and in ours.

We are now in a position profitably to return to the Protozoa, to the phases of cell-life, and to the sex-elements. After what we have just said, it is evident that there are but three main physiological possibilities,—preponderant anabolism, or predominant katabolism, or an approximate (*i.e.*, oscillating) equilibrium between these tendencies. A growing surplus of income, a lavish expenditure of energy, or a compromise in which the cell lives neither far below nor quite up to its income. Great passivity, great activity, or a safe average between these; conservative accumulation, spendthrift liberalism, and a compromise between these. In many different ways, more or less metaphorical, we may express the plain and indubitable facts of anabolism and katabolism within the living matter. The student may think of the processes, with some degree of accuracy, under the metaphor of a ceaseless fountain, which, while remaining approximately constant, is the expression of continual ascent and descent of drops. The protoplasm

itself must often be in as ceaseless change as the apex of the jet.

In active, motile, ciliated, or flagellate cells, whether they be constant forms or only phases, there is relatively predominant katabolism,—predominant when compared with the life expenditure of a passive, quiescent, enclosed, or encysted cell. In amœboid organisms these extremes are avoided; there is certainly great amplitude of variation still, but neither anabolism nor katabolism gains the ascendant in any marked degree.

Suppose, then, in such an amœboid cell, a continued surplus of anabolism over katabolism, the result is necessarily a growth in size, a reduction of kinetic energy and movement, an increase in potential energy and reserve food-material. Irregularities will tend to disappear, surface-tension too may aid, and the cell acquires a spheroidal form. The result—surely intelligible enough—is a large and quiescent ovum.

It will be remembered that young ova are very frequently amœboid; that with a copious nutrition this disappears in varying degrees of encystment; that ensheathing envelopes arising from the ovum, sweated off like cysts round Protozoa, are exceedingly common; and that ova are the largest of all animal cells.

Starting once more from an amœboid cell, if katabolism comes to be more and more marked, the increasing liberation of kinetic energy thus implied must find its outward expression in increased activity of movement and in diminished size; the more active cell becomes modified in form, in adaptation to passage through its fluid environment, and the natural result is a flagellate sperm.

In short, then, the respective morphological characters of the sex-cells, female and male, find the same physiological rationale as do the large passive encysted and smaller active ciliated phases of the cell-cycle in general, and are alike the outcome and expression of predominant anabolism and katabolism respectively. Here again we reach the same formula as before; or, more cumbrously in words—the functions are either self-maintaining or species-maintaining, individual or reproductive; the former are divided into anabolic and katabolic, the latter into male and female. But the second set of products and processes, so far from being unrelated to the other, as is commonly supposed, are in complete parallelism. Femaleness is relative anabolic preponderance in reproduction,

hence the ovum has necessarily the general character which this "diathesis" produces in non-reproductive cells; and, similarly, relative katabolic preponderance stamps its character of active energy upon the spermatozoon as naturally as upon the ciliated cell or the monad.

Here and throughout it must be remembered that we are dealing with relative preponderance of anabolism or katabolism,—with *ratios* in metabolism. The more exact expression of our point is that the ratio $\frac{A}{K}$ in the female is greater than the ratio $\frac{A}{K}$ in the male.

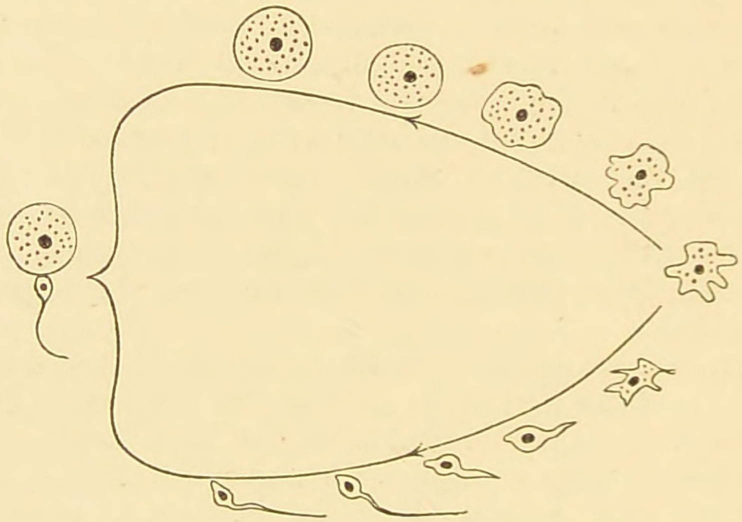


Diagram showing the divergence of ovum and spermatozoon from an undifferentiated amœboid type of cell.

Rolph's characterisation of the male cells as hungry and starving (katabolic) has been experimentally confirmed by their powerful attraction to highly nutritive fluids, and is every day illustrated in their persistent attraction to the ova. Platner has suggested, in the intimately hermaphrodite gland of the snail, that the external cells which form the ova are better nourished than the central cells which divide into sperms. Just as an infusorian in dearth of food is known in some cases to divide into many small individuals, so the mother-sperm-cell is perhaps the seat of similar katabolic necessities. The long persistence of vitality seems at first sight a difficulty, if the sperms are highly katabolic cells. It must be noticed, however, (*a*) That there is often only retention, not continuance of activity, *e.g.*, when the sperms lie closely packed in the special storing reservoirs; (*b*) That the secretions of the female ducts probably afford some nutriment to the sperms, which expose an exceptionally large surface in proportion to their mass; and (*c*) That to a certain extent we may think of them as protoplasmic explosives, which may remain long inert, but on the presence

of the required stimulus are able to start again into extraordinary activity. That they have, like the exhausted infusorians in Maupas's experiment, reached the limit of their dividing power, is also evident. We might refer, for instance, to Von Bardeleben's observations of futile attempts at division (cytokinesis without karyokinesis) in the final stages of spermatogenesis in man ("Jena. Zeitschr. Nat.," xxxi., 1898, pp. 475-520, 3 pls., 5 figs.).

Professor Giard has discussed the question of the possible parthenogenesis of the male elements or microgametes ("Comptes Rendus Soc. Biol. Paris," 1899). He suggests that the phenomena observed by Delage, and termed "merogonic," where a non-nucleated ovum-fragment, fertilised by a spermatozoon, proceeds to develop normally, may be regarded as cases where the microgamete or sperm-cell develops parthenogenetically. Siedlecki has observed the parthenogenetic development of the microgamete of the Sporozoon *Adelea ovata;* the same, as Klebs and others have shown, may occur in the lower plants.

§ 3. *The Problem of the Origin of Sex.*—We must now return once more to the standpoint of the empirical naturalist, and set out towards the interpretation of sex from a different side, that of its origin.

It has often been raised as a reproach against the now fortunately dominant school of evolutionist naturalists, that they could give no account of the origin of sex; and it must be admitted that there have not been many vigorous attempts to tackle the problem. Apart from the simple fact, that evolutionist biology is still young, there are three reasons for the comparative silence in regard to the problem of sex.

(1.) The first of these is the prevalent opinion, that when one has explained the utility or advantage of a fact, one has sufficiently accounted for it. This opinion rests on an acceptance of the selection theory, and on a willingness to cover all questions of origin with a frank "ignoramus," or with the vague assumption of an indefinite variability which affords selection sufficient material to work upon. Our attempt is to push the postulate of indefinite variability as far back as possible, and to suggest a physiological reason why the variations which have led to sex-dimorphism should have taken the lines which they presumably did. It is evident that a preoccupation with the ulterior benefits of the existence of sex may somewhat obscure the question of how male and female have in reality come to be.

(2.) A second reason for the comparative silence may be found in the fact that the problem remains insoluble until it is analysed into its component problems. The question of the

origin of sex to a mind unprepared for the consideration of such a problem, suggests quite a number of difficulties,—What is the import and origin of sexual reproduction (the setting apart of special cells)? what is the meaning and beginning of fertilisation (the interdependence and union of sex-cells)? what is the reason of the individual, male or female, sex in any one case (the determination of sex)? and lastly, what is the nature and origin of the difference between male and female?—the question at present under discussion. For purposes of analysis, these questions must be kept distinct.

(3.) A third reason why the problem of the origin of male and female has been so much shirked, why naturalists have beaten so much about the bush in seeking to solve it, is that in ordinary life, for various reasons, mainly false, it is customary to mark off the reproductive and sexual functions as facts altogether *per se*. Modesty defeats itself in pruriency, and good taste runs to the extreme of putting a premium upon ignorance. Now this reflects itself in biology. Reproduction and sex have been fenced off as facts by themselves; they have been disassociated from the general physiology of the individual and the species. Hence the origin of sex has been involved in special mystery and difficulty, because it has not been recognised that the variation which first gave rise to the difference between male and female, must have been a variation only accenting in degree what might be traced universally.

§ 4. *Nature of Sex as seen in its Origin among Plants.*—In tracing the origin of sex, we would wish to guard against any impression of having consciously or unconsciously arranged our facts in the light of the theory we hold. Hence we prefer to follow some accessible account, taken essentially from the morphological point of view. We shall follow Professor Vines in his article "Reproduction—Vegetable," in the *Encyclopædia Britannica*, at each stage, however, endeavouring to interpret the facts, physiologically, in the light of protoplasmic processes.

(1.) The simple alga, *Protococcus*, common on tree-stems, in pools, wells, and the like—reproduces itself in a simple fashion. The cell divides into a number of equal units or spores; these are set free, are mobile for a while, eventually come to rest, and develop to the normal size. A hint, however, of the beginning of a difference is seen when the cell occasionally divides into a larger number of smaller spores. These, however, show no difference in history. They settle down, and develop just like their more

richly dowered neighbours. We find here the occurrence of units of smaller size, that is to say, less predominantly anabolic, but still these are able to develop independently.

(2.) In a higher alga, *Ulothrix*—one of the series known as Confervæ—both large and small reproductive cells are developed. The large ones develop always of themselves, and so may the smaller forms. But the smaller forms may also unite in pairs, and then start a new plant from the double capital thus attained. When one of the smaller cells develops by itself, the result, in some cases at least, is a weakly plant. They have what Professor Vines calls an "imperfect sexuality," for while they are in part dependent upon union with other cells, they are not wholly so. They are anabolic enough, we may say, sometimes to develop independently, but often they are individually too katabolic for anything but weak independent development. In uniting, however, in mutual nutrition, they are strong. The student will already see the relative femaleness of the large units, the maleness of their smaller neighbours.

(3.) A third stage is reached in another alga, *Ectocarpus*, which is peculiarly instructive. This may separate off large cells which develop by themselves like parthenogenetic ova. From other parts of the plant smaller units are liberated, which generally, though not yet invariably, unite with one another before developing. But between these smaller units a most important physiological difference has been observed by Berthold. Some soon come to rest and settle down, and with these their more energetic neighbours by-and-by unite. We have here a very distinct beginning of the distinction between male and female elements. The comparatively sluggish, more nutritive, preponderatingly anabolic cells, which soon settle down—are female; the more mobile, finally more exhausted and emphatically katabolic cells—are male. As Vines says, "the one is passive, the other active; the former is to be regarded as the female, and the latter as the male reproductive cell."

(4.) Further, in another alga, *Cutleria*, the differentiation may be traced. Two kinds of units result, which must unite with one another if development is to take place, but these units arise from perfectly distinct sources in the parent plant. The larger less mobile cells, which soon come to rest, are fertilised by the smaller more active units. The more anabolic or female cells are fertilised by the more katabolic or male cells, which have now gone too far for the possibility of independent development.

(5.) To complete the series, we may simply mention such a case as that to which we shall presently return,—those forms of *Volvox*, where an entire colony of cells produces either female or male elements, thus representing the beginning of an entirely unisexual many-celled organism.

While the above cases also involve the problem of the origin of fertilisation, which is left over for the present, they confirm our conclusion that relative predominance of katabolism or anabolism is the characteristic of male or female respectively.

§ 5. *Nature of Sex as seen in Origin among Animals.*—Among the Protozoa also, we can trace the beginnings of the

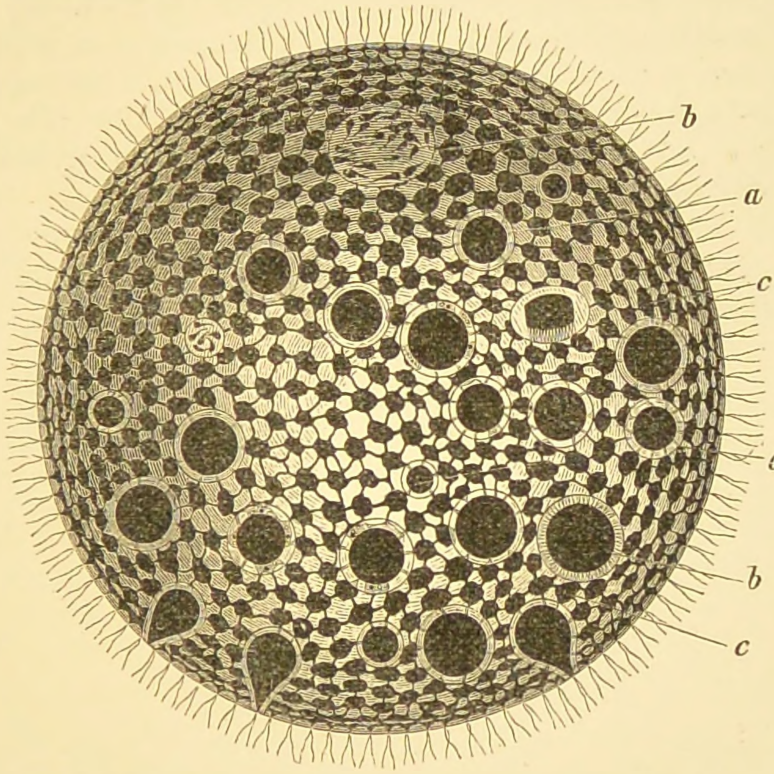
same "dimorphism" between male and female. A union between similar cells is of course frequent, but that is not at present to the point. What we refer to are the numerous cases, especially among flagellate and Vorticella-like infusorians, where the two individuals which unite are quite unlike one another both in form and history. "There can be no doubt," Hatchett Jackson remarks, "that the process is essentially a sexual one; when the individuals are invariably different, there is no reason why the terms male and female should not be applied to them." In some cases we find as before that a small active katabolic unit combines with a larger, more passive, and anabolic individual.

In the bell-animalcule (*Vorticella*), so common on the water-plants of our ponds, a minute free-swimming unit, formed as one of the results of repeated division, unites with a stalked individual of the normal size. In the related *Epistylis*, Engelmann has described how an individual divides first of all into two cells. One of these remains as such (like an ovum), the other repeatedly divides (like a mother sperm-cell) into numerous minute units. One of these subsequently unites with the undivided cell, and Engelmann does not hesitate to call the different elements male and female. In some radiolarians (*e.g.*, *Collozoum*) dimorphic spores—large and small—have been described, although their history has not yet been fully traced.

As another illustration, it will be instructive to select the case of *Volvox*. In this colonial organism, which is best regarded as a multicellular protist, the component cells are at first all alike. They are united by protoplasmic bridges, and simply form a vegetative colony. In favourable environmental conditions this state of affairs may persist, or be interrupted only by parthenogenetic multiplication. When nutrition is checked, however, sexual reproduction makes its appearance, and that in a manner which illustrates most instructively the differentiation of the two sets of elements. Some of the cells are seen differentiating at the expense of others, accumulating capital from their neighbours; and if their area of exploitation be sufficiently large, emphatically anabolic cells or ova result; while if their area is reduced by the presence of numerous competitors struggling to become ova, the result is the formation of smaller, less anabolic cells, which become ultimately *male*, segment into antherozoids, meantime losing their vegeta-

tive greenness and becoming yellow. In some species, distinct colonies may, in the same way, become predominantly anabolic or katabolic, and be distinguished as completely female or male colonies. Thus, again, we reach the conclusion, of a predominant anabolism effecting the differentiation of female elements, and of katabolism as characteristic of the male.

§ 6. *Conclusion.*—In conclusion, in defiance of Dr Minot's dictum, that "such speculation passes far beyond the present possibilities of science," we believe that the consideration (*a*)



Volvox globator, a colonial Alga or Infusorian, showing the ordinary cells (*c*) that make up the colony (or body), and the special reproductive cells (*a*, *b*), both male and female.—After Cohn.

of the characteristics of the sex-elements, alike in history, as Minot himself emphasises, and in their finished form, (*b*) of the incipient sex dimorphism seen among the simplest plants and animals, (*c*) of phenomena, both normal and pathological, in the sexual tissues and organs, (*d*) of the established facts in regard to the determination of sex (chap. 4), and (*e*) of the structural and functional, primary and secondary characteristics of the sexes (chap. 2 and *passim*)—all lead to the conclusion, that the female is the outcome and expression of relatively

preponderant anabolism, and the male of relatively predominant katabolism. Corroborations will gradually appear in the succeeding sections, as we discuss fertilisation, parthenogenesis, or special facts like menstruation and lactation.

The late Mr G. J. Romanes criticised our thesis as a mere re-statement of the facts of sexual dimorphism without any explanation of them. But no other course is open to such inquiries but that of re stating. Our whole point is that of re-stating the idea of dimorphism in protoplasmic terms, at a deeper level of analysis than heretofore, in kinetic terms instead of static ones, and in such a way that the origin and evolution of sex are seen to be not phenomena *per se*, specialised, as naturalists have commonly thought, from the rest of the organism, but congruent with the origin and evolution of other organic differences. From another point of view, we may say that we are seeking to re-state the phenomena of sex by a deeper recognition of the unity of the organism, and of organisms.

SUMMARY.

1. Suggested theories of the nature of male and female; their number and vagueness. Three recent developments—(*a*) Rolph's penetrating suggestion of more nutritive females, less nutritive males; (*b*) Minot's theory of the differentiation of both kinds of sex cells from a primitive hermaphroditism; (*c*) the conclusion of Brooks, that the males are more variable, and alone transmit new variations.

2. Nature of sex seen in its essence in the sex-cells. The fundamental protoplasmic antithesis illustrated in the Protozoa, in the cells of higher animals, in life-histories. The conception of a cell-cycle. The physiological import of this,—the protoplasmic possibilities, preponderant anabolism, predominant katabolism, and a relative equilibrium. The anabolic character of the ova. The katabolic character of the sperms.

3. The problem of the origin of sex, so little tackled, because of (*a*) the *logical* sufficiency of the selection theory and pre-occupation with inquiries as to the utilitarian justification of the facts, (*b*) the number of separate problems involved, (*c*) the isolation of sex and reproduction from the general life of the organism and species.

4. A series from simple plants, showing the gradual appearance of dimorphic sex-cells, with the physiological interpretation thereof. The dimorphism is the result of relatively preponderant katabolism and anabolism, and this is the origin of male and female.

5. Illustrations of incipient dimorphism or sex among the Protozoa. Special reference to the case of Volvox.

6. General conclusion,—(*a*) from the sex-cells, (*b*) from incipient sex, (*c*) from organs and tissues, (*d*) from the determination of sex, (*e*) from the characters of the sexes,—that male and female are the results and expressions of relatively predominant katabolism and anabolism respectively.

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BOOK III.

PROCESSES OF REPRODUCTION.

CHAPTER XI.

SEXUAL REPRODUCTION.

§ 1. *Different Modes of Reproduction.*—It is well known that a starfish deprived of an arm can replace this by a fresh growth; that crabs can renew the great claws which they have lost in fighting; and that, even as high up as the lizards, the loss of part of a leg or a tail can be made good. In a great variety of cases, but decreasingly as we ascend from lower to higher organisms, there is reparation of external injuries. Generally speaking, the facts bear out Lessona's generalisation that regenerative processes are adaptive, occurring in those animals and in those parts of animals in which mutilation tends in the natural course of life to be frequent. Now this "regeneration," as it is called, is in a certain degree a process of reproduction. By continuous growth the cells of a persistent stump are able to reproduce the entire member. We know too that a sponge, a hydra, or a sea-anemone may be cut into pieces, with the result that each fragment grows into a new organism. The same is done with many plants; and though these multiplications are artificial, they illustrate what Spencer and Haeckel said long ago, that reproduction is but more or less discontinuous growth. So again, we pass onwards insensibly from cases of continuous budding, as in sponge or rose-bush, to discontinuous budding in hydra, zoophyte, and tiger-lily, where the offspring, vegetatively produced, are sooner or later set free. Similarly in the Protozoa, an almost mechanical breakage begins the series. This becomes more definite, in the production of several buds at once, or of only one. Budding leads on to ordinary division, both multiple and binary: while finally, in colonial forms, the liberation of special reproductive units may be observed.

§ 2. *Facts involved in Sexual Reproduction.*—It is necessary, at the outset, to be quite clear as to the occurrence of several distinct facts in any ordinary case of sexual reproduction

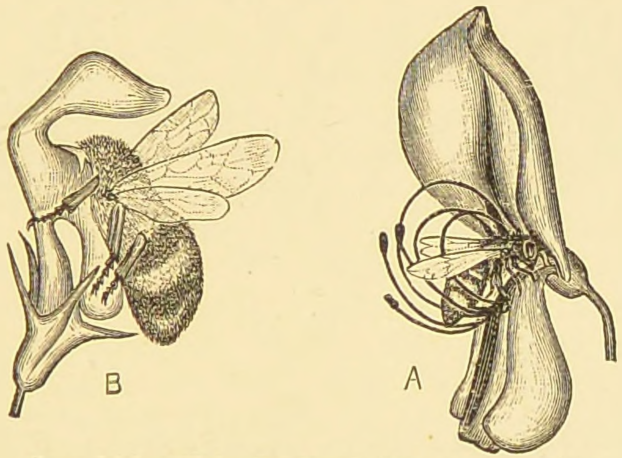
among many-celled organisms. (1.) There is, first of all, the fact that special reproductive cells are present in more or less marked contrast to the ordinary cells making up the body. To this antithesis we have already given due prominence. (2.) Then there is the further fact, that these special reproductive cells are dimorphic; that they, and the organisms which produce them, are distinguishable as male and female. This has been the main theme of the two preceding books. (3.) Lastly, we have to recognise that these dimorphic sex-cells are mutually dependent,—that if the egg-cell is to develop into an organism, it must first be fertilised by a male element. On the facts of fertilisation, therefore, as observed in plants and animals, attention must now be concentrated.

§ 3. *Fertilisation in Plants.*—"The Newly Discovered Secret of Nature in the Structure and Fertilisation of Flowers," so ran the title of a work published by Conrad Sprengel in 1793, embodying his pioneer investigations on a now familiar field. Though not indeed the first to point out the importance of insects in relation to fertilisation,—for that honour appears to belong to Kölreuter (1761),—Sprengel laid sure foundations, now somewhat hidden by the superstructure which Darwin and others have built. To Sprengel's eyes, the many ways in which the nectar is protected from rain seemed full of "intention." He recognised in the markings of the petals illumined finger-posts to lead insects to the hidden hoards; and he further demonstrated that in some bisexual flowers it was physically impossible for the pollen from the stamens to pass to the tips of the carpels. His general conclusion, freely stated, was, that "since a large number of flowers have the sexes separate, and probably at least as many hermaphrodites have the stamens and carpels ripening at different times, nature appears to have designed that no flower shall be fertilised by its own pollen." A few years later (1799), Andrew Knight maintained that no hermaphrodite flower fertilises itself for a perpetuity of generations.

Sprengel's secret of nature had, however, to be set forth afresh by Darwin, who, in his "Fertilisation of Orchids" (1862), and "Effects of Cross- and Self-Fertilisation" (1876), has not only shown, with great wealth of illustration, the manifold devices for ensuring that insects unconsciously carry the fertilising pollen from one flower to another, but has also emphasised the advantage of cross-fertilisation for the health

of the species "Nature tells us," he says, "in the most emphatic manner that she abhors perpetual self-fertilisation." Hildebrand, Hermann Müller, Delpino, and others, have, with consummate patience of observation, further traced out the secrets of nature in this relation; and the student may be referred to D'Arcy Thompson's valuable edition of Müller's "Fertilisation of Flowers," Sir John Lubbock's "Flowers in Relation to Insects," the classic works of Darwin, and P. Knuth's "Handbuch der Blütenbiologie," 2 vols., Leipzig, 1892. Reference must, however, also be made to Meehan's protest (see pp. 80, 81), that self-fertilisation is neither so rare nor so "abhorrent" as is generally believed.

In a great number of cases, cross-fertilisation by means of insects does occur; in many it must occur. In another by no



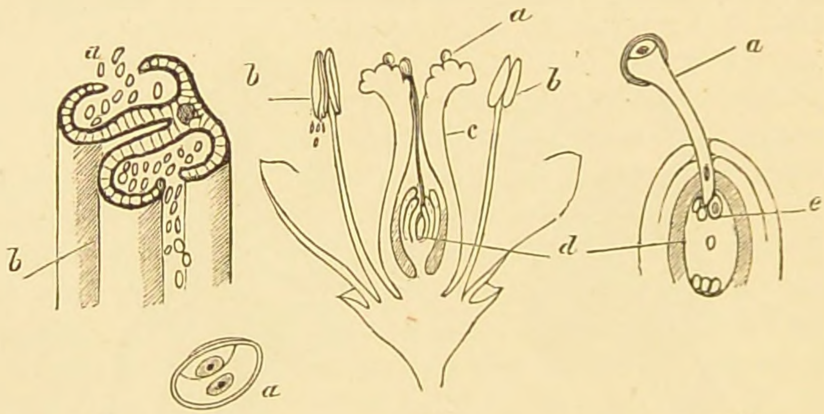
Bees visiting White Deadnettle (B), and Broom (A).

means small set of flowering plants,—usually with inconspicuous blossoms,—the fertilising gold dust is borne by the wind, and falls, like the golden shower on Danaë, upon adjacent flowers. In many hermaphrodite flowers, again, self-fertilisation does certainly take place; in some this is necessarily so. Indubitable self-fertilisation occurs in the small degenerate unopening (cleistogamous) flowers of some plants, such as species of balsam, deadnettle, pansy, &c. These occur along with ordinary flowers, and, curiously enough, are sometimes more fertile than they.

In most of the lower plants, the male elements are minute, and actively mobile. They find their way through the water, or along capillary spaces between the leaves, to the passive female cells. In some cases there is a curvature of the male

organ towards an adjacent female organ, apparently in obedience to chemical or physical attraction. Even here close fertilisation seems exceptional, and is often impossible.

So far, however, only the external aspect of the process. So long ago as 1694, Camerarius showed that if the male flowers of hemp, maize, and other plants were removed, the female flowers bore no seeds, or at least no fertile ones. In 1704, E. F. Geoffroy castrated certain plants by removing the stamens, and noted that they remained barren. "Mirandum sane," he wrote, "quam similem servet natura cunctis in viventibus generandis harmoniam." Reasonable as this now appears to us, the fundamental fact was not only slowly recognised, but on into the present century there were found



A, Enlarged section of ripe Anther (*b*), liberating pollen (*a*). B, Diagrammatic section of a Flower, showing pistil (*c*),—receiving stigma, conducting style, ovary with seed (*d*); the stamens (*b*) with pollen. C, The Pollen-tube (*a*) growing down to the ovule (*d*) and female cell (*e*). The pollen-grain is here represented as distinctly two-celled.

naturalists who strongly opposed it, and denied the sexuality of plants altogether. In 1830, however, Amici made a great step. He traced the pollen-grain from its lighting on the carpel tip down into the recesses of the ovule. Schleiden, whose name is so closely associated with the founding of the "cell theory," soon confirmed Amici's observation, but in doing so went unfortunately much too far. Not only did the pollen-grain send its tube into the ovule, but there, according to Schleiden, it gave origin to the future embryo. This opinion, which, as Heyer observes, made the male element really female, was obviously parallel to that of the zoologists who found in the "sperm-animalcule" the miniature embryo. The view of

Camerarius and Amici of course prevailed; and we now know not only the fact that the pollen-grain is a male element which unites in fertilisation with a female cell, but, thanks especially to Strasburger, much about the intimate nature of the process. In the last century, Millington emphasised the difference between male and female flowers, and we can trace the influence of this discovery in Erasmus Darwin's "Loves of the Plants."

In the last few decennia, it has been shown, for many of the lower plants, that fertilisation essentially involves the union of the nuclei of male and female cells. By analogy the same was believed to be true of higher plants, but direct demonstration has only recently been forthcoming. Strasburger has followed the whole history of the pollen-grain, from the anther of the stamen to the embryo-sac of the carpel; and though some details still remain obscure, his researches have undoubtedly succeeded in elucidating the essential facts in the process. He shows how the pollen-grain divides into a vegetative and a generative cell, of which only the latter is directly important in fertilisation. The generative cell, which consists like the sperm mostly of nucleus with very little directly associated cell-substance, itself divides to form two (or even more) generative nuclei. One of these passes from the pollen-tube to enter into close union with the nucleus of the female cell, with which it fuses to form the double nucleus ruling the forthcoming development. Exceptionally the other generative nucleus may also unite with the nucleus of the egg-cell, but this is almost as rare as "polyspermy" among animals. According to Strasburger, the cell-substance of the pollen-grain or pollen-tube which surrounds the nucleus has no direct influence in the essential act. Fertilisation is a union of two nuclei, "the cell-substance of the pollen-tube is only the vehicle." He confirms the observations of Pfeffer, as to the reality of an osmotic attraction between at least the surroundings of the two essential elements, in accordance with which the pollen-tube bearing the generative nucleus is marvellously guided to its destination. The differentiation of the generative nucleus, in contrast to the more vegetative, and the true nuclear union which forms the climax of fertilisation, are two very important facts, showing the unity of the process not only in higher and lower plants but in all organisms.

Although there are peculiarities distinguishing the processes

of maturation and fertilisation in plants from those observed in animals, it is impossible to deny the essential parallelism. A discussion of this would lead us into technical details, which cannot be profitably described without abundant figures, but we may refer, for instance, to a comparative survey by Professor V. Haecker ("Biol. Centralblatt," xvii., 1897, pp. 689-705, 721-745, 40 figs.). One of the most striking botanical discoveries of recent years is the fact demonstrated by Hirase and Ikeno, that in the Ginkho (*Salisburia adiantifolia*), and in *Cycas revoluta*,—gymnosperm flowering plants belonging to the family of Cycads,—the male nuclei issue from the pollen-tube as motile spermatozoa or antherozoids. Webber has also announced a similar discovery in the case of *Zamia integrifolia*.

§ 4. *Fertilisation in Animals.*—That the sperms are essential to fertilisation was a conclusion by no means recognised when those elements were first seen. Gradually, however, the fact was demonstrated, both by experiment and observation. Jacobi (1764) artificially fertilised the ova of salmon and trout with the milt of these forms, and somewhat later the Abbé Spallanzani extended these experiments to frogs and even higher animals. Even he, however, believed that the seminal fluid was the essential factor, not the contained spermatozoa. Through the experiments of Prévost and Dumas (1824), Leuckart (1849), and others, attention was directed to the real import of the sperms, which Kölliker referred to their cellular origin in the testes. The presence of the sperm within the ovum was observed in the rabbit ovum by Martin Barry in 1843; by Warneck, in 1850, for the water-snail, a fact confirmed about ten years afterwards by Bischoff and Meissner; in the frog ovum by Newport (1854); and in successive years it was gradually recognised in a great variety of animals.

The adaptations which secure that the sperms shall reach the ova are very varied. Sometimes it seems almost a matter of chance, for the sperms from adjacent males may simply be washed into the female, as in sponges and bivalves, with the nutritive water-currents. In other cases, especially well seen in most fishes, the female deposits her unfertilised ova in the water; the male follows and covers them with spermatozoa. Many may have watched from a bridge the female salmon ploughing along the gravelly river bed depositing her ova, careful to secure a suitable ground, yet not disturbing the already laid eggs of her neighbours. Meanwhile she is attended

by her (frequently much smaller) mate, who deposits milt upon the ova. In the frog, again, the eggs are fertilised externally by the male just as they leave the body of his embraced mate. Or it may be that the sperms are lodged in special packets, which are taken up by the female in most of the newts, surrounded with one of the male arms in many cuttle-fishes, or passed from one of the spider's palps to the female aperture. In the majority of animals, *e.g.*, insects and higher vertebrates, copulation occurs, and the sperms pass from the male directly to the female. Even then the history is very varied. They may pass into special receptacles, as in insects, to be used as occasion demands; or, in higher animals, they may with persistent locomotor energy work their way up the female ducts. There they may soon meet and fertilise ova which have been liberated from the ovary; or may persist, as we noticed, for a prolonged period; or may eventually perish.

When the sperms have come, in any of these varied ways, into close proximity to the ovum, there is every reason to believe that a strong osmotic attraction is set up between the two kinds of elements. We have often suspected that the approach of the conjugating cells of two *Spirogyra* filaments might be directed along the line of an osmotic current; and although we must confess that perhaps somewhat rough evaporations, performed a few summers ago, gave no positive confirmation to the idea that glucose or the like might be present in appreciable quantity in the water, a recent observer, we are glad to see, claims to have been more fortunate.

The spermatozoa, which seem so well to deserve Rolph's epithet of "starved," appear to be powerfully drawn to the well-nourished ovum, and the latter frequently rises to meet the sperm in a small "attractive cone." Often, however, there is an obstacle in the way of entrance in the form of the egg-shell, which may be penetrable only at one spot, well called the micropyle. Dewitz has made the interesting observation that round the egg-shells of the cockroach ova, the sperms move in regular circles of ever-varying orbit; and points out that thus, sooner or later, a sperm must hit upon the entrance. He showed that this was a characteristic motion of these elements on smooth spheres, for round empty egg-shells or on similar vesicles they moved in an equally orderly and systematic fashion.

The persistence with which the spermatozoa often force their

way to the ova makes it impossible to doubt the reality of a strong chemotactic attraction. One illustration may suffice. According to Dr Sadone's account of the impregnation in the Rotifer *Hydatina senta* ("Zool. Anzeiger," xx., 1897, pp. 513-17), the spermatozoa of the male, which are injected into the body-cavity of the female, reach the totally enclosed eggs by boring through the thin membrane at a point where the mature ova are situated—a process not known in any other animals. The oval head of a spermatozoon was seen to attach itself to the membrane of the ovary, the tail continued to make lashing movements, the head was gradually forced through the membrane, and the tail followed, the whole process taking about ten minutes.

It was till recently believed that more than one sperm might at least enter the ovum, but researches such as those of Hertwig and Fol have shown that when one sperm has found admittance, the way is usually barred against others. The micropyle may be blocked, or the surrounding membrane may be altered, or in other ways the ovum may exhibit what Whitman calls "self-regulating receptivity," so as to be no longer penetrable. We are safe in concluding,—that the ovum is usually receptive only to one sperm; that in most cases the entrance of more than one sperm is impossible; and that where "polyspermy" does occur, pathological development is at least often the result.

It may be well to note that there are, as in plants, various steps in the process which is often roughly summed up in the one word—fertilisation.

(1) There is the process by which the spermatozoa are brought into general proximity to the ova. In higher animals this is best termed insemination, and is accomplished by copulation.

(2) There is the approach of the spermatozoon to the ovum, but of this little is known.

(3) There is fertilisation in the strict sense,—the intimate and orderly union of two sex-nuclei.

What takes place before fertilisation is, as we have just seen, very varied indeed among animals; what takes place after fertilisation is of course cell division, but that, though referable to certain great types, must necessarily be very diverse; what takes place in the act of fertilisation, however, is always essentially the same. The head of the spermatozoon becomes the male nucleus (or pro-nucleus) of the fertilised ovum, entering into close association with the female nucleus. The latter, as we have

already noted, has had its own history; it is no longer the original germinal vesicle, nor usually like it in appearance, it is the germinal vesicle minus the quantity of nuclear substance given off in forming two polar globules. This female nucleus (or pro-nucleus, as it is generally called) comes into close association with the sperm or male-nucleus; nor does it remain quite passive in the process, though the greater activity in bringing about the close association is certainly still exhibited by the male. Whitman has recently emphasised the reality of an attractive influence between the pro-nuclei. Fusion of the pro-nuclei was observed so long ago as 1850 by Warneck in the pond-snail (*Lymnæus*). The result, however, appears to have been overlooked, till the same fact was reobserved in threadworm ova by Bütschli in 1874. Since that date the fact has been continuously studied. Some observers still doubt whether what can be accurately called fusion of nuclei ever occurs; and if fusion means inextricable confounding and mixing up of the male and female nuclear elements, it is almost certain that such does not in any case happen. There is no doubt, however, that the two nuclei become very closely associated, and according to most observers a double unity is formed, in which the component nuclear elements from the two origins so diverse are united in perfectly orderly fashion. So exact, in fact, is this duality, that when the first division of the egg takes place, each of the two daughter-cells has in its nucleus half of the male and half of the female elements, and so on perhaps in after-stages.

The object upon which the intimate phenomena of fertilisation have been most studied is the ovum of the threadworm (*Ascaris megalocephala*) which infests the horse. Since 1883 numerous important memoirs have dealt with this subject, and with the same material. The general results stand out clearly, though there remain not a few minor discrepancies. To one of these, now explained, we may briefly refer. According to Van Beneden, the normal ovum of the threadworm contained in its nucleus one chromatin element, and was fertilised by a sperm also with one chromatin element. Carnoy, however, described the normal ovum as containing two chromatin elements, and as fertilised by a sperm also with two. In view of the perfection with which both these investigators had unravelled the structure and behaviour of the nuclei, the discrepancy seemed serious enough. But Boveri has shown that both are right; Van Beneden's type occurs; Carnoy's type also occurs. Nay more, an ovum with one chromatin element seems to be always fertilised by a sperm with only one, while an ovum with two chromatin elements is fertilised by a sperm likewise with two.

A few of the details may be summarised from the masterly researches of Boveri. The extrusion of the two polar cells from the ovum is in reality a double process of cell-division. The quantity of the nuclear substance in the germinal vesicle is thereby reduced, and the number of nuclear elements is also reduced to half the normal. Only one sperm penetrates the ovum, unless the latter be unhealthy; and with the entrance of the sperm the ovum undergoes a simultaneous change, which excludes other male elements. Only the head or nuclear portion of the sperm is of real importance in the essential act of fertilisation; the nutritive tail or cap simply dissolves away. After the sperm-nucleus has penetrated to the centre of the ovum, and after the extrusion of the polar bodies is quite completed, we have to deal with two nuclei, not only closely approximate in structure, but alike in further history.

In Carnoy's type, both male and female nuclei contain two chromatin elements, in the form of bent rods; and before union takes place, these undergo a marked modification, the same in both cases. Round the chromatin rods vacuoles are formed, limiting them from the surrounding protoplasm; into these the rods send out anastomosing processes, after the fashion of little rhizopods; gradually the rods thus resolve themselves into a network, in the meshes of which minute "nucleoli" are also demonstrable.

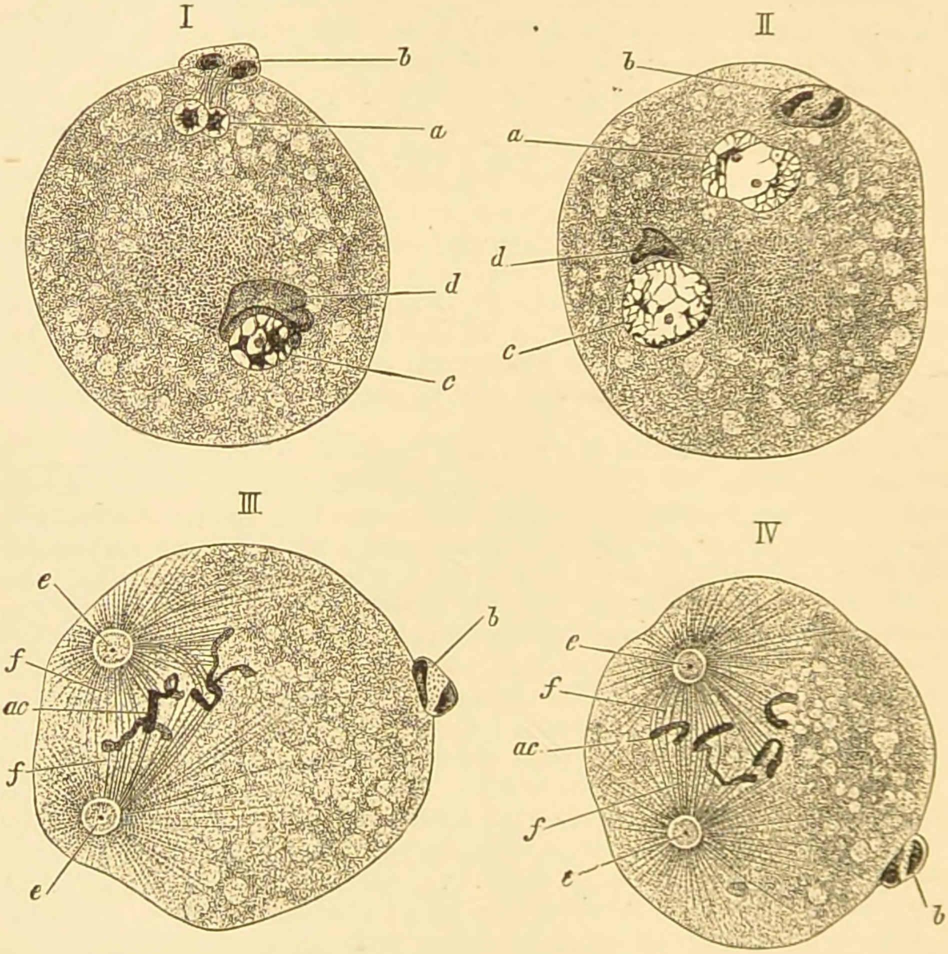
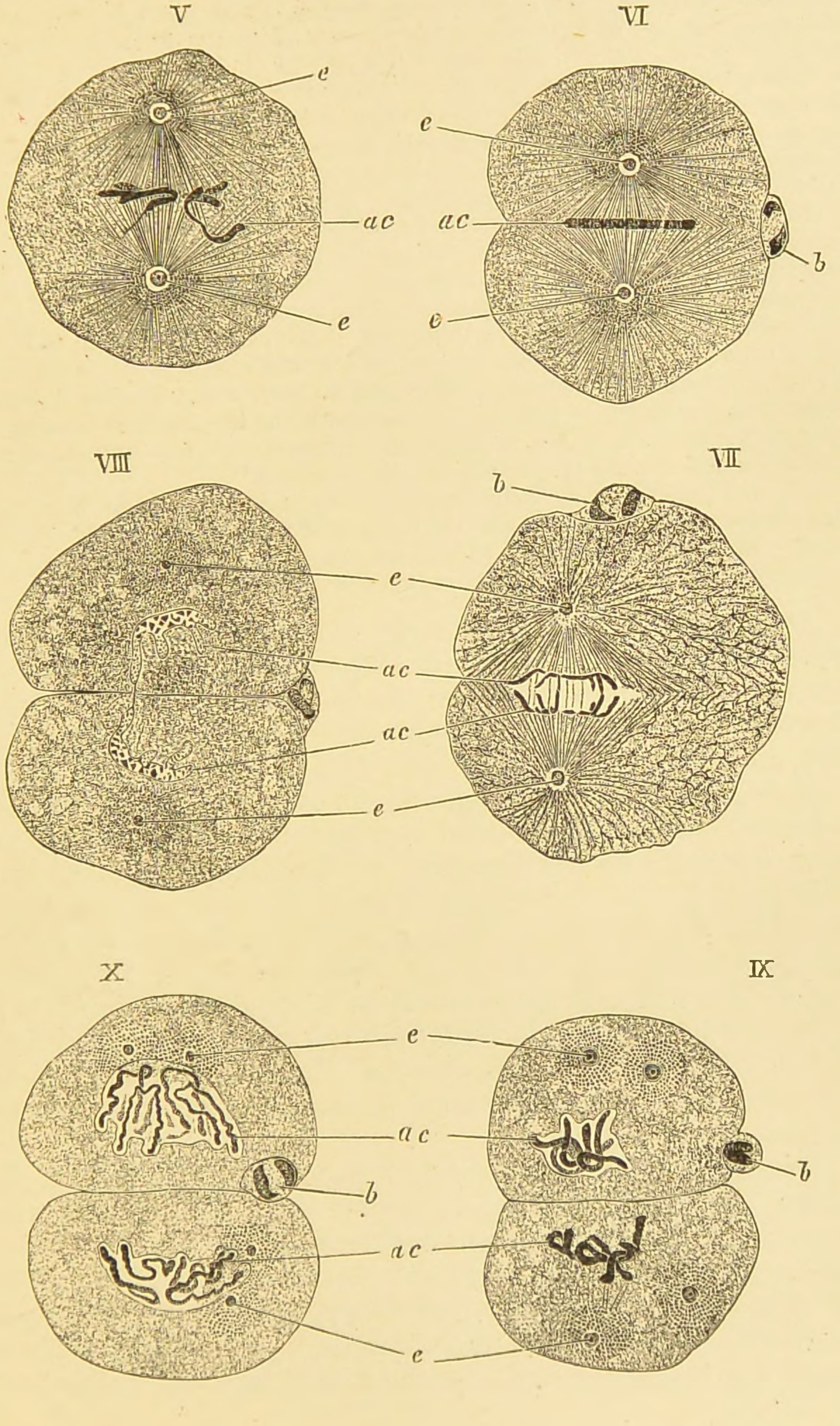


Diagram of the Process of Fertilisation, after Boveri.—*a*, female pro-nucleus; *b*, polar bodies; *c*, male nucleus; *d*, sperm-cap; *ac*, chromatin elements of united female and male nuclei (*a* and *c*); *e*, centrosomes; *f*, archoplasmic threads.

The two nuclei thus modified then unite, but that again so precisely, as Van Beneden especially has shown, that each forms half of that spindle figure which almost all nuclei take when about to divide. This double spindle figure is the "segmentation nucleus," which will presently divide into the two first daughter-nuclei of the ovum (see figs. VI.-X.).

It is not possible here to discuss certain intricate changes which take place meanwhile, not in the nuclei, but in the cell-substance of the ovum. Both Van Beneden and Boveri have recently agreed on the existence of two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"central corpuscles" (centrosomata) in the protoplasm. These serve as "points of insertion" for protoplasmic threads, which exert a "muscular action" upon the nuclear elements in the forthcoming division. Boveri has traced with great care the history of a special kind of protoplasm (what he calls the archoplasm), which has its centre in either "central corpuscle" (*c*), and sends out fibrils (*f*), which moor themselves to the nuclear elements. The movements of the latter during the forthcoming first division of the ovum are directly referable to the antagonistic action of these fibrils, and thus we have hints of an intracellular muscularity.

In the spindle the nuclear elements, still distinguishable in their orderly behaviour as male and female, eventually form what is known as the "equatorial plate" (VI.), lying across the centre of the spindle. This is a well-marked stage, and one characterised by apparent equilibrium. "It is the resting-stage *par excellence* in the life of the cell. Movement is at an end, a state of stability has set in, and this would continue *ad infinitum*, did not a factor, which hitherto has played no part, assert itself and bring about fresh movement. This new movement is the longitudinal division of the chromatin elements, an independent expression of life—indeed, a reproductive act—on the part of the nuclear elements."

Of each longitudinally split chromosome one half moves or is moved towards the one centrosome, and the other half towards the other centrosome. After this apparently equal partition a nuclear reconstruction is gradually effected, and the ovum reaches the 2-cell stage.

One marvellous fact, showing the closeness of union in fertilisation, may be briefly re-emphasised. In the double nucleus formed from the union of male and female nuclei, Van Beneden, Carnoy, and others, have shown that both constituents have an equal share. The one half is paternal, the other maternal, and this is true not only for *Ascaris* (Van Beneden) and other threadworms (Carnoy), but for representatives of other worm-types, cœlenterates, echinoderms, molluscs, and tunicates. In the division which forms the first two daughter-cells (IX., X.), half of each set of constituents goes to either cell, and the dualism is kept up. Furthermore, it is probable that of the chromatin loops observed in the division figure of a daughter-cell, half are derived from the male parent, and half from the female. The importance of this fact, in relation to the influence of both parents upon the offspring, is very obvious.

One of the clearest of modern exponents, Professor E. B. Wilson, who has himself made important contributions to the subject, sums up the present-day view of the matter in the following sentences:—"From the mother comes in the main the cytoplasm of the embryonic body, which is the principal substratum of growth and differentiation. From both parents comes the hereditary basis or chromatin by which these pro-

cesses are controlled, and from which they receive the specific stamp of the race. From the father comes the centrosome to organise the machinery of mitotic division by which the egg splits up into the elements of the tissues and by which each of these elements receives its quota of the common heritage of chromatin. Huxley hit the mark two score years ago when he compared the organism to a web, of which the warp is derived from the female and the woof from the male. What has since been gained is the knowledge that this web is to be sought in the chromatic substance of the nuclei, and that the centrosome is the weaver at the loom." (See "The Cell in Development and Inheritance," 1896, p. 171.)

The above short sketch will show how intricate, and yet at the same time how orderly, are the intimate processes of fertilisation. Variations do indeed occur, both in pathological and in apparently normal cases; but a general constancy is now both clear and certain, not only for many different animals, but also to a certain extent, as Strasburger and others have shown, for plants.

§ 5. *Fertilisation in Protozoa.*—In the nascent sexual union observed in many Protozoa, considerable diversity obtains. The individuals which unite may be to all appearance similar (to which cases the term conjugation is generally applied), or they may be materially dimorphic, as in *Vorticella.* The union may be permanent, when the two units fuse into one; or it may only be temporary, during which an interchange of elements takes place. The union may be complete, as in the conjugation of two Gregarines, or partial, as in the slipper-animalcule, and between these may be placed the state of affairs observed in various species of bell-animalcule (*Vorticella*), where the nuclei and the bulk of the smaller conjugate pass into the larger, leaving, however, shrivelled remains which are cast off. This, as described by Hs. Wallengren ("Biol. Centralblatt," xix., 1899, pp. 153-161, 3 figs.), shows that the distinction between total and partial conjugation is only one of degree. In many cases the nuclear elements are seen to play an important part, disrupting and reconstructing during the process, while a genuine fusion of the two nuclei has also been observed in permanent conjugation.

In regard to the interchange of elements, there is considerable divergence of observation. Joseph has noted what appears to be an interchange of protoplasm; Schneider has observed the exchange of nuclear elements; while Gruber and Maupas, and Joseph as well, have, in their studies on the union of ciliated infusorians, laid emphasis on an accessory nuclear body, generally known as the "micro-nucleus." This body lies by the side of the larger nucleus, and while the latter simply disrupts and dissolves away, or is extruded without playing any important part, the smaller micro-nucleus divides in a regular way, and with the results there is micro-nuclear interchange between the two individuals.

According to Maupas, who has investigated the subject in most detail,

the para- or micro-nucleus is a "hermaphrodite" sexual element, of sole importance in conjugation. The stages in the process of fertilisation are as follows:—

(1.) The micro-nucleus increases in size.

(2.) Division occurs until there are eight micro-nuclei.

(3.) Of these eight, seven disappear.

(4.) The remaining one divides again, differentiating a male and female pro-nucleus.

(5.) In the next stage, the male elements of the two individuals are exchanged, and the new male nucleus fuses with the original female portion.

(6, 7.) In two following stages, the nuclear dualism characteristic of the ciliated infusorians is re-established. The old large nucleus (macro-nucleus) has broken up and been eliminated meanwhile.

(8.) Finally, the individuals, separating from one another, reassume all their original organisation before beginning again to divide in the usual fashion.

The union of the male and female nuclear elements in ciliate infusorians was admirably figured by Balbiani so long ago as 1858; and though he does not seem rightly to have interpreted what he observed in this particular case, he was right in his contention that sexual union and fertilisation really occurred in the Protozoa. Balbiani's view has been for long scouted, and yet, with renewed observation, naturalists have now come back to his conclusion. Maupas willingly allows that Balbiani figured beautifully what he himself has since reobserved and interpreted.

The phenomena described by Maupas, as summarised above, have been observed in towards a dozen ciliated infusorians, so that there is every reason to believe in their general occurrence. In three species of the slipper-animalcule (*Paramœcium*), and in species of *Stylonichia*, *Leucophrys*, *Euplotes*, *Onychodromus*, *Spirostomum*, &c., the facts are as above stated.

It is of interest to cite the facts in regard to the common bell-animalcule (*Vorticella*), because here the conjugating individuals are like ovum and sperm in more ways than one. In some species—*e.g.*, *V. monilata*—the adult divides equally, to form two small individuals, which conjugate with those of normal size. In *V. microstoma* there is again division into two, but the products are of unequal size; one is much smaller than the other. In the nearly allied *Carchesium polypinum*, the divisions are equal, but they are repeated twice or thrice. The result in all cases is the production of minute individuals, which eventually attach themselves to adults of the normal size, first to the stalk, and then to the body. The accessory nuclear bodies divide as usual; the large individual ceases to feed, and hermetically closes its mouth, like an ovum when fertilised. The small individual is gradually absorbed by the larger, as sperm by ovum; and in an intricate but orderly fashion a mixed nucleus results from the fusion of the micronuclear elements of the two. The adult then begins to feed, to divide, and so on, as usual. Here then there is (*a*) incipient dimorphism, (*b*) absorption of smaller by larger, and (*c*) intimate nuclear union,—facts which we have already emphasised in the fertilisation of multicellular animals.

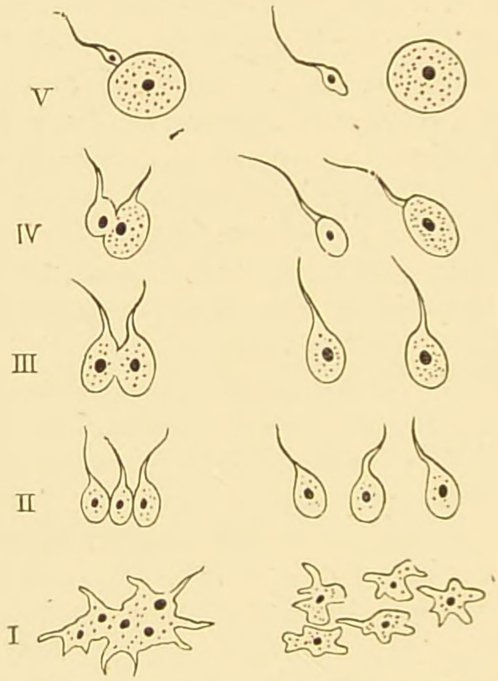
§ 6. *Origin of Fertilisation.*—To understand the origin of the union of sex-cells, attention must still be concentrated on

the Protozoa. That fertilisation really occurs at that low level in a highly complex fashion, we have just seen. It is necessary, however, to note the steps which lead up to what Maupas and others have so patiently elucidated.

(*a*) In the primitive life-cycle exhibited by *Protomyxa* (see fig. at p. 129), the units which burst forth from the cyst sink down into tiny amœbæ, and unite together in numbers to form a composite spreading mass of protoplasm, technically known as a *plasmodium*. This is undoubtedly a very primitive union of cells, yet it occurs at very diverse levels in the organic series. It is more or less familiar in the "flowers of tan," one of the lowly Myxomycetes, where a nucleated mass of protoplasm, of composite origin, spreads over the bark in the tan-yard. The plasmodial union also occurs as a definite stage in the life-history of the primitive neighbours of *Protomyxa*, the Monera of Haeckel. Pour the liquid contents or body-cavity fluid of a freshly-dredged and still actively living sea-urchin into a bowl; the cells which float in it, like blood-corpuscles in the blood, draw together in clotted masses. Watch the process under a microscope, and the formation of a plasmodium is seen. The dying cells fuse into composite masses, just like the units of *Protomyxa;* and it is interesting to observe that, though they are dying, the union provokes a brief but intense renewal of amœboid activity. To forestall our point, they as it were *fertilise* each other in *articulo mortis*. In spite of the objection of Michel and others, that such union, being pathological, is not comparable to the multiple conjugation normal to the myxomycete, we maintain the distinct analogy between the plasmodium formation in Myxomycetes and that exhibited by the cells in the body-cavity fluid of many animals, and regard this as so much additional evidence of the profound unity of the normal and the pathological processes. Now it is from this primitive union of cells, as illustrated in the lowest organisms, that we start in explaining the origin of fertilisation. Just as the very beginning of reproduction seems almost like mechanical breakage, so the very beginning of fertilisation is found in the almost mechanical flowing together of exhausted cells.

(*b*) Between this and the process usually described as conjugation, there are some interesting links. Sometimes as many as three or four spores of lowly Algæ club together, as if to gather sufficient momentum to make a combined start in life.

The young forms of the sun-animalcule (*Actinosphærium*) usually unite in twos, but Gabriel has observed in some cases a multiple union. In another sun-animalcule (*Actinophrys sol*) two to thirty individuals may unite loosely in what is often called plastogamy, but close union (of nuclei) only occurs between two individuals. So in gregarines (common parasites in invertebrates), while the usual union is certainly dual, Gruber has again observed what may be termed multiple conjugation. Union of three has also been observed as an exception in



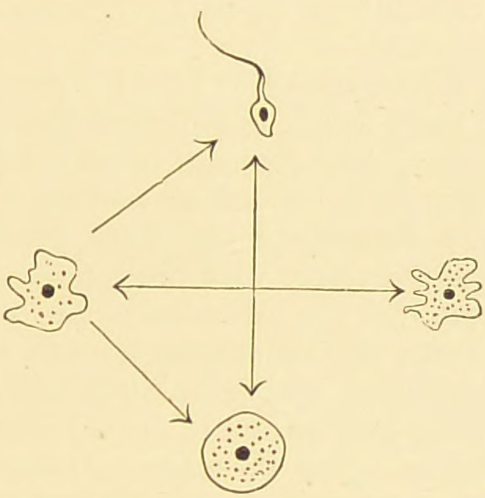
Diagrammatic representation of the stages in the origin of fertilisation,—(I.) plasmodium; (II.) multiple conjugation; (III.) ordinary conjugation; (IV.) conjugation of dimorphic cells; (V.) fertilisation of ovum by spermatozoon.

several infusorians. The union of more than two may thus be interpreted as intermediate between the formation of plasmodia and the normal dual conjugation.

(*c*) Conjugation of two *similar* unicellular organisms occurs, as we have seen, very generally in the Protozoa, and is also a common fact in the life-history of simple Algæ. It is open to every one possessed of a microscope to observe what conjugation means in such a common fresh-water alga as *Spirogyra*. Opposite cells of adjacent filaments are attracted to one another, and the contents of the one cell pass bodily over into the other.

In the great majority of cases where conjugation occurs, the uniting cells are to all appearance similar, but it must be remembered that it does not follow from this that they are physiologically alike.

(*d*) Both among plants and animals, all naturalists are agreed that it is impossible to draw any line between the conjugation of similar and the union of more or less dimorphic elements. "This differentiation presents," Sachs says, "especially in Algæ, a most complete series of gradations between the conjugation of similar cells and the fertilisation of oospheres by antherozoids, any boundary line between these two processes being unnatural and artificial." The gradual appearance of



Diagrammatic representation of the contrast between conjugation (horizontal line) and fertilisation (vertical line).

dimorphism has been already noted in discussing the origin of sex, and need not be re-emphasised.

(*e*) Lastly, in fertilisation among higher plants and animals, the two elements which unite are highly differentiated, alike in contrast to one another and in opposition to the general cells of the body. A consideration of the phenomena in loose protist colonies like *Volvox* or *Ampullina*, which suggest the bridge between unicellular and multicellular organisms, shows how gradually this latter contrast also may have been brought about.

To sum up, the steps in the development of the process of fertilisation may be arranged in the following series :—

(*a*) The formation of plasmodia.

(*b*) Multiple conjugation.

(*c*) Conjugation of two similar cells.
(*d*) Union of incipiently dimorphic cells.
(*e*) Fertilisation by differentiated sex-elements.

One difficulty must in fairness be allowed in connection with the hypothesis of deriving conjugation from plasmodial union. Some years ago, Sachs was inclined to regard the plasmodium formation of Myxomycetes as a process of multiple conjugation, but he afterwards withdrew this mainly on the ground that the nuclei have not been shown to coalesce. Now there seems no result of studies on fertilisation more certain than that the union of nuclei is an essential fact, but in plasmodium formation, such intimate association of nuclei cannot be asserted. The difficulty of making this a starting-point is thus at first sight considerable.

Yet it must be observed, (1) that our knowledge of the nuclei in those lowly forms is still very inadequate; (2) that, according to Gruber, the behaviour of the nucleus is sometimes masked by the fact that, instead of existing as a discrete body in the cell, it lies diffusely in the protoplasm; but especially (3) that it is quite consistent with the general evolutionary conception to suppose that the primitive union was of very much less definite character than that subsequently evolved.

Even in conjugation *nuclear* union is not always clear. It is well known in the conjugation of Infusorians, but it has been very rarely proved in other Protozoa. It has been observed, however, in some cases, *e.g.*, by Wolters, in the common *Monocystis* of the earthworm, and by Schaudinn, in the sun-animalcule, *Actinophrys sol.*

Rhumbler has made an elaborate study of the possible evolution of fertilisation-processes. He finds the first step in cytotropism, in which chemotropic substances are secreted between cells, and in this connection we must bear in mind the experiments of Klebs, which show that the addition of various reagents to the culture-solution in which a simple Alga or Mould is living will determine the occurrence of sexual or asexual reproduction. The next step is plastogamy,—two naked cells become apposed and fuse. At a higher level, karyogamy is reached. ("Biol. Centralbl.," xviii., 1898, pp. 21-26, 33-38, 69-86, 113-130, 14 figs.).

§ 7. *Hybridisation in Animals.*—Many of the compound names of animals, such as leopard, point back to a once prevalent belief that animals of very different kinds might unite sexually and have fertile offspring.

Only to a very limited extent is such a notion justified. Every one is aware that by direct human control animals like horse and ass, dog and wolf, lion and tiger, hare and rabbit, canary and finch, pheasant and hen, goose and swan, have been successfully crossed. In nature, however, we know relatively little of the occurrence and results of any such hybridisation. It seems to occur in some fishes; different species of toad are often seen in sexual union; it is said to be not uncommon between various species of birds and insects.

M. André Suchetet, after many years' study of hybridism in birds and mammals, stated the following provisional conclusions ("Journ. de l'Anat. Physiol.," xxxiii., 1897, pp. 326-355):—

(1) Cases of hybridism in mammals number about 93, of which 82 are (*a*) crosses of species of the same genus, and 11 are (*b*) doubtful cases of crosses between members of different genera. There is no instance (*c*) of crossing between members of distinct families or widely-separated genera. Among birds, 262 cases are recorded, 178 of the first category (*a*), 68 of the second (*b*), and 16 (some doubtful) of the third (*c*).

(2) Of the 82 crosses between mammals of distinct species but of the same genus, the great majority (62) resulted in sterile offspring. In about 12 cases, the offspring have proved fertile with one of the parent species or with a third species. In 7 or 8 cases the offspring have proved fertile *inter se*, sometimes for three or four generations.

Among birds, in 178 crosses between members of distinct species but of the same genus, only 22 resulted in fertile offspring, 8 *inter se*, the others with the parent species, or with a third species, or with other hybrids.

Of the 68 crosses between species of different genera but of the same family, only one had offspring fertile with one of the parent species—the male hybrid of *Columba livia* × *Turtur risorius* was fertile with the female of the latter species. The female hybrid resulting from the same cross seemed sterile. In two other cases a hybrid of this category fertilised a third species; in another case it was fertilised by this third species.

(3) As to the causes of the sterility in the hybrid offspring, the reproductive organs are sometimes atrophied, in other cases the ducts are abnormal, but there remain many instances in regard to which we can only shroud our ignorance with the word "constitutional."

In some cases hybridisation succeeds readily, in other cases it is very difficult to bring it about. Thus Mr H. M. Vernon found that in some Echinoderms—*Sphærechinus* and *Strongylocentrotus lividus*—hybridisation occurred very readily and was highly successful. In some nearly related frogs, on the other hand, it always fails. In certain cases the cause of the difficulty is almost mechanical; thus Pflüger showed that the spermatozoa of *Rana fusca*, which have very pointed heads, thinner than those of related forms, can fertilise the eggs of nearly all other species (*R. arvalis*, *R. esculenta*, and *Bufo communis*), but the blunt, thick-headed spermatozoa of *R. arvalis* and *R. esculenta* cannot fertilise the eggs of any other species. On the other hand, Hertwig's experiments on sea-urchins point to the conclusion that the state of the egg is very important in determining whether the hybridising will succeed or not. Eggs in good condition resist the entrance of spermatozoa to which the stale ova prove receptive. It should also be noticed that fertilisation and segmentation may occur without further development. This was Born's experience in many cases

with amphibians, and T. H. Morgan had the same result with the ova of a starfish fertilised by the spermatozoa of a sea-urchin; segmentation proceeded, a hybrid gastrula was formed, but no further progress was made.

There is no doubt that at least many species-hybrids tend to sterility, but this is exhibited in varying degrees. The male mules are always sterile, but some say that the females may be successfully impregnated by horse or ass. In many cases hybrids are not fertile with one another, but remain so with the parent form. In a few cases the reproductive functions seem for a time at least to be exaggerated rather than diminished as the result of crossing.

It seems also certain that while variety-hybrids are usually fertile, their constitution is often unstable. They are often very variable, and apt to die out, as has been repeatedly observed in the human species. The ill-natured saying, "God made the white man, God made the black man, the devil made the mulatto," refers to the frequently inconvenient variability of those variety-hybrids. It is impossible, however, to generalise this. All that can be said is that some cross-fertilisations are very disadvantageous, while others seem to be as markedly the reverse.

Brooks has laid considerable emphasis on the variability of hybrids in connection with his theory of heredity. "Hybrids and mongrels," he says, "are highly variable, as we should expect from the fact that many of the cells of their bodies must be placed under unnatural conditions, and must therefore have a tendency to throw off gemmules." "Hybrids, from forms which have been long cultivated or domesticated, are more variable than those from wild species or varieties, and the children of hybrids are more variable than the hybrids themselves." "But domesticated animals and plants live under unnatural conditions, and they are therefore more prolific of gemmules than wild species; and as the body of a male hybrid is a new thing, the cells will be much more likely than those of the pure parent to throw off gemmules. The fact that variation is due to the male influence, and that the action upon the male parent of unnatural or changed conditions results in the variability of the child, is well shown by crossing the hybrid with the pure species; for when the male hybrid is crossed with a pure female, the children are much more variable than those born from a hybrid mother by a pure father." It cannot be said, however, that the evidence is as yet sufficient to warrant these general conclusions.

In successful hybridisation, three results are common:—(*a*) a blending of the parental characters, (*b*) more or less exclusive expression of the characters of one parent, and (*c*) a form quite unlike either parent. What direction the new variation will take cannot be predicted, but in many cases the result is a re-appearance of the characters of an ancestral form. In some cases this may mean that latent characters which have for a time been unexpressed are permitted to develop; in other cases it may mean that a new permutation of qualities has independently reproduced an old pattern or combination. Herr von Guaita found that if the Japanese dancing mouse was crossed with an albino, the second generation consisted of grey mice like the wild forms. ("Ber. Nat. Ges. Freiburg," x., 1898, pp. 317-332.)

Professor Cossar Ewart took a pure white fantail cock-pigeon, which in colour had proved prepotent over a blue pouter, and paired it with a cross previously made between an "owl" and an "archangel," and the result

was a couple of fantail-owl-archangel crosses, one resembling the Shetland rock-pigeon and the other the blue rock of India. Again, a smooth-coated white rabbit, derived from an Angora and a smooth-coated white buck, was mated with a smooth-coated, almost white doe (grand-daughter of a Himalaya doe); and the result was that in a litter of three, one was the image of the mother, a second was an Angora, like the paternal grandmother, and one was a Himalaya, like the maternal great-grandmother. For further details "The Penycuik Experiments" (1899) should be consulted.

The hybrid offspring often resembles one of its parents much more than the other. Thus Standfuss found that in reciprocal crossing the male is able to transmit the characters of its species in a higher degree than the female. A reverse result is noted below.

The relative maturity of the two sex-elements has been shown by Vernon to be of importance in the hybridisation of sea-urchins. The characters of the offspring incline to be those of the species whose elements were relatively the more mature when fertilisation occurred.

Standfuss has also noted that the freshly hatched larva often closely resembles the female parent; that with growth a resemblance to the male parent gradually increases; and that the final extent of approximation towards the male parent depends on the relative phylogenetic age of the two species, the older being able to transmit its characters, whether of structure or habit, better than the young.

In pairing normal forms with varieties and local races, Standfuss found (1) that when the norm ("*Grundart*") is crossed with a gradually formed local race of the same species, the result is a series of intermediate forms; but (2) that when the norm is crossed with a sporadic variety, the result in many cases is that the issue agrees either with the norm or with the sport, intermediate forms being absent. ("Handbuch der paläarktischen Gross-Schmetterlinge," 2nd ed., Jena, 1896.)

In short, the result seems to depend on the issue of what may be called the germinal struggle between hereditary characters of varying strength.

The results reached by Standfuss are not altogether corroborated by other workers. Thus J. W. Tutt gives an account ("Trans. Entomological Society, London," 1898, pp. 17-42) of experiments made by Riding and Bacot in hybridising two allied species of *Tephrosia—T. bistortata* Goeze (*crepuscularia* auct.) and *T. crepuscularia* Hb. (*biundularia* auct.). The hybrids show all degrees between full fertility and complete sterility; they may be fertile *inter se* and with the parent stock; the phylogenetically older species is more dominant in stamping its characters on the progeny and the female parent more than the male; a recently formed variety may be prepotent over the type from which it has sprung. The re-crossing of a hybrid with one of the parent species produces offspring scarcely differing from that parent species; the inbreeding of the same cross produces a large percentage differing much from either parent form; the crossing of the hybrids obtained from original reciprocal crosses tends to produce a mixed progeny, some referable to known forms of the crossed species, others quite unlike anything ever obtained in nature.

Henri Gadeau de Kerville calls attention to an interesting conclusion—requiring, however, to be more carefully substantiated—that the results of successful hybridisation are much oftener males than females, and that male offspring are more numerous in proportion to the specific distance

between the two parents ("Bull. Soc. Zool. France," xxiv., 1899, pp. 49-51).

The early researches of Kölreuter (1761) gave a firm basis to the study of hybridisation among plants. The comparative easiness of experiment has advanced the botanical side of the subject to far greater certainty than the zoological conclusions can pretend to. Among plants, as we should expect from their greater vegetativeness, the fertility of hybrids seems frequently established. Knight, Gārtner, Herbert, Wichura, and others, have brought together a great number of reliable observations, and the whole subject has been admirably discussed by Nägeli. For a copious resumé of the general results, for the most part after Nägeli, the student may be referred to chap. vi. of Sachs' Text-book of Botany, while Wallace's "Darwinism" should be consulted for its rediscussion of hybridisation in animals.

§ 8. *Telegony.*—The belief has been for long current among breeders that the effective impregnation of a female may influence not only the immediate offspring, but subsequent offspring by a *different* sire. It is said that a pure-bred bitch lined by a mongrel dog is thereby spoiled for future breeding. The supposed influence is technically called telegony, and the supposed facts are usually explained by supposing that the surplus sperms in the first impregnation exert an influence on the immature ova in the ovary, or by supposing (in mammals) that the mother is affected by her first offspring through the medium of the placenta. The first point, however, is to make sure that there are facts to be explained, and this seems very doubtful. What has been regarded as the influence of the first sire on the offspring of the same mother by a second sire may receive some other explanation, may be, for instance, an independent variation, or may be simply a reversion. Much, if not most, of the alleged evidence is anecdotal; and careful experiments made by Professor Cossar Ewart, on the lines of Lord Morton's famous case, have yielded no evidence of the reality of telegony.

Dr Otto vom Rath has suggested ("Biol. Centralbl.," xviii., 1898, pp. 637-642) that the occurrence of badly-bred pups in a litter, which breeders regard as the result of telegony, may be accounted for by co-infœtation, in which case different sires are supposed to fertilise the ova which may be shed into the oviduct at intervals of several days. But this, again, requires further proof.

SUMMARY.

1. Reproduction is but more or less discontinuous growth.

2. Sexual reproduction normally implies (*a*) special reproductive cells, distinct from the body; (*b*) the dimorphism of these cells; (*c*) their physiological dependence,—the ovum being unproductive without the spermatozoon, and *vice versâ*.

3. The discoveries of Camerarius, Amici, Kölreuter, Sprengel, and others, laid the foundations of our knowledge of sexual reproduction in plants.

4. The history of research on fertilisation in animals well illustrates the gradually increasing precision of scientific inquiry.

5. The conjugation processes seen in Protozoa are of much importance in suggesting the origin of differentiated fertilisation.

6. The origin of fertilisation may be traced through the following grades:—(*a*) plasmodial union, (*b*) multiple conjugation, (*c*) ordinary conjugation, (*d*) union of dimorphic cells, (*e*) fertilisation of ovum by spermatozoon.

7. Both in plants and animals hybridisation is often successful, but the offspring frequently tend to be sterile. This, however, must not be exaggerated.

8. Telegony has not been demonstrated.

LITERATURE.

See the already noted works of Balfour, Van Beneden, Carnoy, Geddes, Haddon, Hensen, Hertwig, M'Kendrick, Sachs, Vines, and Wilson.

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CHAPTER XII.

Theory of Fertilisation.

In his 49th Exercitation on the "efficient cause of the chicken," Harvey thus quaintly expresses what has always been, and still is, a baffling problem:—"Although it be a known thing subscribed by all, that the fœtus assumes its original and birth from the male and female, and consequently that the egge is produced by the cock and henne, and the chicken out of the egge, yet neither the schools of physicians nor Aristotle's discerning brain have disclosed the manner how the cock and its seed doth mint and coine the chicken out of the egge."

§ 1. *Old Theories of Fertilisation.*—(*a*) From Pythagoras and Aristotle on to the "Ovists," of whom we have already spoken, numerous naturalists have held the opinion that the ovum was the all-important element, which only required to be awakened to development by contact with the male fluid or male elements. It must be allowed, that while ova may exceptionally develop without sperms, the latter never come to anything apart from ova.

(*b*) In contrast to the above opinion, we find ingenious thinkers, so widely separate in time as Democritus and Paracelsus, regarding the male fluid as very important, forestalling Buffon and Darwin in fact in considering it in a sense an extract or concentrated essence of the whole body. But it was only after the spermatozoa were themselves detected that their importance became unduly exaggerated, in the minds of those who seem almost to have been nicknamed "animalculists." It seems probable enough that Leeuwenhoek himself (1677) saw the spermatozoon entering the ovum,—he at least said that he did,—but that did not prevent him from ascribing to the male elements all the credit of development. This became, as we have seen, a favourite hypothesis, and imagination supplied more than modern magnifiers to those observers who

detected in the spermatozoon the members and lineaments of the future organism.

(*c*) The third opinion, that both elements are of essential and inseparable import, is obviously alone consistent with the facts. This view also has had its gradual development, only one phase of which need be noticed. Even after the nature of the spermatozoa as male-cells was recognised, that is to say, even since the middle of the nineteenth century, an old conception of the male influence lingered persistently. This namely, that contact was not essential, but that a "sort of contagion," a "breath or miasma," "a plastical vertue," "without touching at all, unless through the sides of many mediums," was sufficient to effect what we call fertilisation. The above expressions are used by Harvey, who further says, "this is agreed upon by universal consent, that all animals whatever, which arise from male and female, are generated by the coition of both sexes, and so begotten as it were *per contagium aliquod*." De Graaf attempted in vain to give more precision to this "contagion" in his theory of an "*aura seminalis*," or seminal breath which passed from the male fluid to the ovum. But the conception of an "aura" was only a verbal cloak for that absence of definite knowledge which the slow progress of observation still necessitated. The theory was partly strengthened by a number of erroneous observations, which seemed to show that successful fertilisation could occur when the genital passages of the female were apparently blocked by malformation or disease. Spallanzani gave a death-blow to the theory of an "aura," by showing experimentally that contact of the male fluid with the ovum was absolutely necessary. Even he, however, went away from the true conclusion, by maintaining that the fertile male fluid of toads was destitute of spermatozoa. That the above vague conceptions have been replaced by the certain conclusion, that intimate cellular union is the *sine qua non* of fertilisation, we have already emphasised.

§ 2. *Modern Theories of Fertilisation—Morphological.*—Recent investigators of the facts of fertilisation have generalised their results in different ways according to their dominant bias. Some mainly restrict themselves to stating the morphological facts, and to emphasising the relative importance of cell-substance and of nuclei in the union; others attack the deeper problem of the physiological import of the process,—a problem

the full solution of which is still remote; while others have confined themselves rather to discussing the uses of fertilisation in relation to the species. Some representative positions on each of these planes must be sketched; and, first of all, the more morphological theories, and the very important question whether the union of nuclei is everything, or whether the union of cell-substance has also its import.

(*a*) *Hertwig's View.*—Professor O. Hertwig, who was one of the first carefully to follow out the details of fertilisation in animals, thus sums up his "*Theorie der Befruchtung*":—"In fertilisation, distinctly demonstrable morphological processes occur. Of these the important and essential one is the union of two sexually differentiated cell-nuclei, the female nucleus of the ovum and the male nucleus of the sperm. These contain the fertilising nuclear substance, which is an organised substance, and acts as such in the process. The female nuclear substance transmits the characters of the mother, the male nucleus those of the father, to the offspring." The nucleus is thus the essential element both in fertilisation and in inheritance.

(*b*) *Strasburger's View.*—What Hertwig maintains for animals, Strasburger does for plants. "The process of fertilisation depends upon the union of the sperm nucleus with the nucleus of the egg-cell; the cell-substance (cytoplasm) does not share in the process." "The cell-substance of the pollen-grain is only the vehicle to conduct the generative-nucleus to its destination." It may become nutritive, he allows however, to the germ-rudiment. "Generally the uniting nuclei are almost perfectly alike," though there may be slight differences in the size of the nucleoli. "The two cell-nuclei do not differ in their nature, they are not sexually differentiated in the ways that the individuals are from which they originate. All sex-differentiations only serve to bring together the two nuclei essential to the sexual process."

The opinions of these two authorities are certainly representative, and they both agree in emphasising that the nuclei are all-important, and that it does not matter much about the union of cell-substance. Some objections to this view must be noticed. (*a*) It is permissible to doubt whether the recent concentration of attention upon the nucleus has not led to some under-appreciation of the general protoplasm. In the permanent conjugation of two cells, the entire contents of the two cells are obviously fused; and even when the union is temporary, Joseph has observed what looks like an interchange of protoplasmic as well as of nuclear substance. (*b*) There are a few observers still, such as Nussbaum, who maintain that in fertilisation in animals the substance of the sperm is important as well as its nucleus. (*c*) Strasburger notes the minimal quantity of cell-substance so often present round the male nucleus, and urges that if it were important there would surely be more of it. But it is quite conceivable that a minimal quantity of highly active protoplasm might have, like a ferment, a momentous influence on a large quantity of a different character. (*d*) It is, moreover, a very probable view that cytoplasm and nucleus attain their full significance only in inter-relation, forming what has been called a "cell-firm." (*e*) Boveri made the delicate experiment of removing the nucleus from a sea-urchin ovum which he afterwards fertilised. Although

the ovum had therefore only paternal nuclear material it developed into a larva. More recently Delage has extended the experiments and has reared normal larvæ of sea-urchin, worm (*Lanice*), and mollusc (*Dentalium*) from non-nucleated ovum-fragments which were successfully fertilised. He describes this remarkable phenomenon under the title of merogony. (*f*) The researches of Boveri and others show that the sperm brings with it into the ovum a protoplasmic centre—a "centrosome"—which appears to be of much importance in the preparation for division. In this preparation, according to Boveri, the "muscular fibrils" of a special kind of protoplasm (or archoplasm) literally move the nuclear elements. "The movement of the elements is wholly the result of the contraction of the attached fibrils, and the final arrangement of these nuclear elements in the 'equatorial plate' is the result of the action of the archoplasmic sphere exerted through the fibrils." Now this specially active protoplasm has its centre in the two central corpuscles, each "ruling a sphere of archoplasm." There seems general agreement as to the fact that the sperm furnishes the centrosomes in at least the majority of cases, and there is no doubt that these minute bodies play a prominent part in the division which follows fertilisation. At this stage, then, it seems rash to deny that even the minimal cell-substance of the spermatozoon may, as well as its nucleus, have a momentous influence in fertilisation.

§ 3. *Physiological Theories of Fertilisation.*—The morphological facts, established and verifiable by observation, form the basis from which to attack the deeper problem of the physiology of fertilisation. Here experiment is almost insuperably difficult; only a few incidental results are as yet available; the suggestions thrown out by various naturalists must therefore be appreciated according to their consistence with the general principles of physiology, and with the general theory of sex and reproduction. To some they may still appear a page of probabilities.

Sachs compares the action of the male element upon the egg-cell to that of a ferment. De Bary also suggests that profound chemical differences exist between the two elements. Very suggestive is the view of Rolph, who regarded the process as essentially one of mutual digestion. His vivid words well deserve quotation:—

"Conjugation occurs when nutrition is diminished, whether this be due to want of light, or to the lowered temperature of autumn and winter, or to a reduction of the organisms to minimal size. It is a necessity for satisfaction, a gnawing hunger, which drives the animal to engulf its neighbour, to 'isophagy.' The process of conjugation is only a special form of nutrition, which occurs on a reduction of the nutritive income, or an increase of the nutritive needs, in consequence of the above-mentioned conditions. It is an 'isophagy,' which occurs in place of 'heterophagy.' The less nutritive, and therefore smaller, hungrier, and more mobile organism we call the male,—the more nutritive and usually relatively more

quiescent organism, the female. Therefore too is it, that the small starving male seeks out the large well-nourished female for purposes of conjugation, to which the latter, the larger and better nourished it is, is on its own motive less inclined." Cienkowski has also inclined to a similar view, regarding conjugation as equivalent to rapid assimilation.

In *Holothuria tubulosa* and some other Echinoderms, N. Iwanzoff has observed ("Bull. Soc. Nat. Moscou," 1897, pp. 355-367, 1 pl.) that immature ova, after a certain stage, show great sexual attraction for spermatozoa, and emit many pseudopodia, while the mature ovum only emits one. But the spermatozoa absorbed by the immature ova are digested, which leads the author to the speculative suggestion that the process of maturation weakens the nutritive vitality of the ovum so that it is unable, fortunately, to digest the spermatozoon.

Simon also seeks to establish the following among other vague conclusions:—Sexuality has, he says, arisen twice (we should say much oftener), once among plants, again among Protozoa. Two similar cells unite "in order to reach the limit of their individuality." In both kingdoms the union is at first protective, though in a different fashion in the two cases. In the progressive differentiation, these two sex-cells are usually so constructed that the loss of substance in the union is reduced to a minimum; hence the small mobile male and the large quiescent female cells. The union brings about a chemico-physical process, which makes the female cell capable of independent nutrition and growth, and evokes potential properties into actual life.

In marked contrast to Rolph's suggestion, and the view of all those who believe that the sex-cells are profoundly different, is the opinion maintained by Weismann. He denies that there is a dynamical action in fertilisation. The momentous effect is merely a restoration of the normal composition of the nucleus. "The physiological values of sperm and egg-cell are equal; they are as 1 : 1. We can hardly ascribe to the body of the ovum a higher import than that of being the common nutritive basis for the two conjugating nuclei." The external differences which are so obvious are only important as means towards the conjugation of similar nuclei. "The germ-plasm in the male and female reproductive cells is identical." Previous to the essential moment of fertilisation, the germ-plasm is reduced in maturation. Development will not take place unless the loss be made good. This is what the sperm does in fertilisation. In short, to Weismann the process is quantitative rather than qualitative.

This supposition appears to us to be open to criticism. (1.) That the nuclei are alone important in fertilisation, and that the cell substance is a mere adjunct, cannot be said to be proved, and we have already noted some of the facts which tell the other way. (2.) The structure of a cell is recognised by all to be an expression of its dominant protoplasmic processes. The sex-cells are usually highly dimorphic, and even Strasburger

allows that there may be minor differences in their nuclei, as well as the marked divergence in their cell-substance. The nucleus cannot be regarded as an isolated element, but as one which shares in the general life of the cell. We have already interpreted the differentiated male and female cells as respectively katabolic and anabolic, and see no reason for doubting, in spite of structural resemblance in the rough features of nuclei (all that we know), that this difference saturates through the elements. (3.) If the only important matter be the quantitative restoration of the original amount of germ-plasma in the female nucleus, it seems difficult to understand the phenomena of conjugation, whether permanent or transitory, from which we believe fertilisation to have originated. (4.) The occasional possibility of inducing division by replacing the sperms with other stimuli, seems to point to a dynamical or chemical action. Thus Loeb induced artificial parthenogenesis in sea-urchin ova by placing them for a couple of hours in sea-water, to which some magnesium chloride had been added. (5.) Delage's evidence that non-nucleated portions of ova may be readily fertilised and form normal larvæ, strongly suggests that the mingling of heritable qualities, which is certainly one of the results of fertilisation, must be distinguished from the physiological stimulus to division.

It is very desirable that the experiment which Piéri has begun of extracting a ferment (ovulase) from seminal matter and using it as a fertilising stuff, should be confirmed or confuted.

It has been already noted, in regard to the origin of fertilisation, that the almost mechanical flowing together of exhausted cells is connected by the stages of multiple conjugation with the ordinary form of the latter, while the respective differentiation of the two elements effects the transition to fertilisation proper. Historically, then, fertilisation may be compared to mutual digestion, and, though bound up with reproduction, it may have arisen from a nutritive want. With the differentiation of the elements on anabolic and katabolic lines, the nature of the fertilising act becomes more definite. The essentially katabolic male cell, getting rid of all accessory nutritive material contained in the sperm-cap and the like, brings to the ovum a supply of characteristic products which stimulate the latter to division. The profound chemical differences, surmised by some, are intelligible as the outcome of the predominant anabolism and katabolism in the two elements. The union of the two sets of products restores the normal balance and rhythm of cellular life. At the same time, it is of course certain that the spermatozoon is the bearer of the inheritable paternal characteristics.

§ 4. *Uses of Fertilisation to the Species.*—Not a few naturalists have passed from the individual aspect of fertilisation to its general import in relation to the life of the species. Why

should fertilisation occur at all, if parthenogenesis in some cases works so well? Part of this question is almost illegitimate, if the existence of male and female be, as we think, simply the expression of a more developed swing of "the organic see-saw" between anabolism and katabolism. The answers have, however, much interest, and are valuable, so long as they are not magnified so as to hide the deeper physiological problems lying below. The origin and physiological import of fertilisation can never be explained by any elucidation of its subsequent advantageousness.

The two naturalists who have recently reached the most valuable results in regard to the results of fertilisation are Maupas and Weismann. This they have done by very different paths,—Maupas, in working out the details of conjugation in infusorians; Weismann, in his wider studies on the problems of heredity and evolution. To Maupas, fertilisation is necessary to prevent the death of the species; to Weismann, fertilisation is the ever-recurrent beginning of new vital changes, and the continual preservation at the same time of the relative constancy of the species. Several naturalists of the highest reputation have regarded fertilisation as a process which supplied a fresh life-impulse to the species. Thus Galton has insisted, with much clearness and force, on the liability of asexual, or what he calls unisexual multiplication to end in degeneration or extinction, and on the necessity of double parentage for the preservation and progress of the species. Similarly, Van Beneden, Bütschli, and Hensen have all spoken of the process as a rejuvenescence (rejeunissement, Verjüngung). The asexual process of cell-multiplication is limited; conjugation in lower, fertilisation in higher organisms supplies the recurrent impulse which keeps the life of the species young. According to Van Beneden,—"The faculty which cells possess of multiplying by division is limited. There comes a time when they can divide no further, unless they undergo rejuvenescence by fertilisation. In animals and plants, the only cells capable of being rejuvenesced are the eggs; the only cells capable of rejuvenescing these are the sperms. All the other parts of the individual are devoted to death. Fertilisation is the condition of the continuity of life. Par elle le générateur échappe à la mort." Hensen, in his admirable "Physiology of Reproduction," expresses the same when he says:—"By normal fertilisation, death is warded off (ferngehalten) from the germ and its

products." Bütschli has interpreted conjugation in similar terms.

Weismann quotes the three opinions just mentioned, and vigorously criticises them. He demands evidence for the limitation of asexual reproduction assumed above, and speaks of the "impossibility of proof." The whole "conception of rejuvenescence has something indefinite and misty about it." "How can one think that an infusorian, which by continued division has at length exhausted its reproductive capacity, will regain the same by uniting and fusing with another which has also lost its power of further division? Twice nothing cannot give one; or if we assume that in each animal there persists only half the reproductive capacity, so that the two together would form one, this one can hardly call 'rejuvenescence.' It would be simply an addition, as is under other circumstances attained by simple growth,—that is, if we leave out of account what in my eyes is the most important moment in conjugation, viz., the mingling of two heredity-tendencies (*Vererbungstendenzen*)." He sarcastically compares the two exhausted individuals to two exhausted rockets, which are supposed to rejuvenesce in mutually affording the constituents of nitro-glycerine. More forcibly he urges the difficulty suggested by continued parthenogenesis,—a difficulty which we shall afterwards have to discuss. "To the conception of rejuvenescence," he says, in conclusion, "I could only agree, if it were proved that multiplication by division can never,—not merely in certain conditions,—but never continue unlimitedly. This cannot, however, be proved, just as little as the reverse." But Weismann must surely admit that the demonstration of even some cases where species, normally reproducing asexually, come to an absolute standstill if conjugation be prevented, would give considerable strength to the interpretation of fertilisation as rejuvenescence. Maupas has given examples of such cases.

The French observer has shown, as we have seen, that a process of fertilisation occurs in ciliated infusorians. By an elaborate process of nuclear division, disruption, elimination, interchange, union, and reconstruction, two "slipper animalcules" fertilise one another. What is the meaning of all this?

Each infusorian, after conjugation, proceeds to divide, but the results are to all appearance the same as it previously produced. There is no special sexually produced generation.

It has been often alleged that the subsequent dividing is

accelerated by conjugation; but Maupas finds that this is not so. The reverse in fact is true,—it is a loss of time. While a pair of infusorians (*Onychodromus grandis*) were indulging in a single conjugation, another had become, by ordinary asexual division, the ancestor of from forty thousand to fifty thousand individuals.

Moreover, the intense internal change preparatory to fertilisation, and the general inertia during subsequent reconstruction, not only involve loss of time, but expose the infusorians to great risk. It seems then like a condition of danger and death rather than of multiplication and birth.

The riddle was, in part at least, solved by a long series of careful observations. In November 1885, M. Maupas isolated an infusorian (*Stylonichia pustulata*), and observed its generations till March 1886. By that time there had been two hundred and fifteen generations produced by ordinary division, and since these lowly organisms do not conjugate with near relatives, there had, of course, been no sexual union.

What was the result? At the date referred to, the family was observed to have exhausted itself. The members, though not exactly old, were being born old. The asexual division came to a standstill, and the powers of nutrition were also lost.

Meanwhile, however, several of the individuals, before the generations had exhausted themselves, had been removed to another basin, where they conjugated with unrelated forms of the same species. One of these was again isolated, and watched for five months. The usual number of successive generations occurred; members removed at different stages were again observed to conjugate successfully with unrelated forms, and this was done on to the one hundred and thirtieth generation. After that, however, the family being again near its end, the removal was no longer any use. About the one hundred and eightieth generation, the strange sight was seen of individuals of the same family attempting to unite with one another. The results were, however, *nil*, and the conjugates did not even recover from the effects of their forlorn hope.

Without the normal sexual union, then, the family becomes senile. Powers of nutrition, division, and conjugation with unrelated forms, come to a standstill. The first symptom is decrease in size, which may go on till the individuals only

measure a quarter of their normal proportions. Various internal structures then follow suit, "until at last we get formless abortions, incapable of living and reproducing themselves." The nuclear changes are no less momentous. The important para- or micro-nucleus may partially or completely atrophy, and conjugation is thus fatally sterile. The larger nucleus may also become affected, "the chromatin gradually disappearing altogether." Physiologically too, the organisms become manifestly weaker, though there is what the author calls a "surexcitation sexuelle." Such senile decay of the individuals and of the isolated family inevitably ends in death.

The general result is evident. Sexual union in those infusorians, dangerous perhaps for the individual life,—a loss of time so far as immediate multiplication is concerned,—is in a new sense necessary for the species. The life runs in cycles of asexual division, which are strictly limited. Conjugation with unrelated forms must occur, else the whole life ebbs. Without it, the Protozoa, which some have called "immortal," die a natural death. Conjugation is the necessary condition of their eternal youth and immortality. Even at this low level, only through the fire of love can the phœnix of the species renew its youth.

The need of extreme carefulness is shown, however, by the somewhat discrepant results reached by D. Joukowsky ("Verh. Nat. Med. Verein Heidelberg," vi., 1898, pp. 17-42). After five months' culture his colony of *Paramœcium caudatum* showed no nuclear degeneration, but only a marked reduction of cilia and a consequent sluggishness. In *P. putrinum* effective conjugation between the descendants of one individual was observed, but the author admits the probability that this has its limits. In another infusorian, *Pleurotricha lanceolata*, over 458 generations were observed without the occurrence of degeneration, and Joukowsky supposes that degeneration depends not on the number of generations merely, but on the rapidity of their successive occurrence.

At the beginning of this century, the too-much-forgotten biologist Treviranus directed attention to fertilisation as a source of variation, and his suggestion has been several times independently revised.

Thus Brooks, to whose works we have repeatedly referred, has emphasised not only the importance of fertilisation as a source of progressive change, but further, that the male element is much the more important in this connection.

Similarly, though on somewhat different lines, Weismann

suggested that the mingling of male and female germ-plasms was a source of those variations on which natural selection operates. "Sexual reproduction is well known to consist in the fusion of two contrasted reproductive cells, or perhaps even in the fusion of their nuclei alone. These reproductive cells contain the germinal material or germ-plasm, and this again, in its specific molecular structure, is the bearer of the hereditary tendencies of the organisms from which the reproductive cells originate. Thus in sexual reproduction, two hereditary tendencies are in a sense intermingled. In this mingling, I see the cause of the hereditary individual characteristics; and in the production of these characters, the task of sexual reproduction. It has to supply the material for the individual differences from which selection produces new species."

Few will be inclined to oppose the thesis that sexual union is productive of variation. To discuss the relations of this view to other theories of variation is beyond our present scope. Thus Weismann has suggested that germinal variations may also arise because of the reducing divisions which precede fertilisation or amphimixis, as he calls it, and furthermore through nutritive and other stimuli which operate through the body upon the germ-plasm. We should also mention Hatschek's suggestion that sexual reproduction is a remedy *against* the operation of injurious variations. We can readily imagine that the excess of some particular line of anabolic or katabolic differentiation may be neutralised through fertilisation, and it may be in this way that the pairing of diseased individuals is sometimes mercifully condoned by nature.

Möbius may be cited here for his vigorous protest against the prevalent idea that continuous vegetative multiplication necessarily results in degeneration. He instances such cases as the banana and date palm, which are never reproduced sexually in cultivation, but it must be remembered that artificial selection is here in operation to sustain the standard. He admits, however, the advantages of sexual reproduction both in conserving the specific characters and in prompting new variations. ("Beiträge zur Lehre von der Fortpflanzung der Gewächse." Jena, 1897.)

In regard to close in-breeding we have still much need of experiment, but it seems fairly certain that with a healthy

stock this may go far without disadvantageous results. It seems rather to fix and strengthen desirable characteristics. On the other hand, if the stock be markedly tainted, the in-breeding is continued at the risk of degeneracy.

Even when the stock is sound to start with, there seem to be limits to close in-breeding, as Vom Rath found in experiments with rats, and Von Guiata in experiments with mice. As many breeders have recorded, there is a tendency to debility, abnormality, and sterility.

According to Reibmayr, the success of a human race is in part dependent on the alternation of periods of sustained in-breeding, which serve to "fix" racial characters, and periods of cross-breeding in which the advantages of "fresh blood" are secured.

SUMMARY.

1. Old theories of "ovists," "animalculists," and of the "aura seminalis."

2. Modern morphological theories incline to lay the whole emphasis upon the nuclei. The conclusions of Hertwig and Strasburger are strongly in favour of this view. The import of the centrosomes and general protoplasm must not, however, be overlooked. Several facts suggest that the all-importance of the nuclei has been exaggerated.

3. Modern physiological theories of fertilisation are necessarily very tentative. Sachs compares it to fermentation; Rolf to mutual digestion. To Weismann, the process appears quantitative rather than qualitative. Suggestion that the male cell brings to the ovum a supply of characteristic chemical substances which act as a stimulus.

4. Uses of fertilisation to the species. Many regard fertilisation as a necessary rejuvenescence of the life of the species. Weismann criticises this view, but his criticism must be read in the light of the researches of Maupas, who has shown that without conjugation the members of an isolated family of infusorians eventually cease to feed and divide, passing through stages of degeneration and senility to extinction. In this case, conjugation is essential to the continued vitality of the species. According to Brooks and Weismann, fertilisation is an important source of variation.

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CHAPTER XIII.

Degenerate Sexual Reproduction or Parthenogenesis.

§ 1. *History of Discovery.*—From very early times there appears to have been an impression, that in exceptional circumstances reproduction might occur without fertilisation. Even Aristotle gave reasons for believing that, without sexual union, the unfertilised eggs of the honey-bee might give rise to perfect adults. We now know that he was right, in his conclusion at least, so far as the development of drones is concerned. In the early belief in *Lucina sine concubitu*, much that was erroneous was intermixed with a prevision of the truth; nor could we expect at an early date that asexual multiplication (*i.e.*, apart from ova altogether) would be kept distinct from what we now mean by parthenogenesis, or the development of ova without union with sperms. In 1701, Albrecht observed that a female silkmoth, which had been isolated in a glass case, laid fertile eggs; and though this was for long discredited, the occasional parthenogenesis of this insect has been repeatedly confirmed by competent observers.

In 1745, the ingenious Bonnet drew attention to what is now a very familiar fact, the successive generations of virgin plant-lice or Aphides. Throughout the summer, he observed the production of numerous generations of these little insects, all females, necessarily therefore all virgins, and yet fertile. So strange did the fact appear, that it was for long utterly discredited. Réaumur eluded the difficulty, by affirming that the Aphides were hermaphrodite; but Dufour soon proved that this was erroneous, though he could only confess his ignorance in referring the phenomena to "spontaneous or equivocal generation," in which "the act of impregnation was in no degree concerned." The facts, however, were repeatedly re-observed. Kirby and Spence admitted them as incontestable, but could regard them only as "one of the mysteries of the Creator, that human intellect cannot fully penetrate."

Meanwhile Schäffer had observed the occurrence of parthenogenesis in minute aquatic crustaceans, the study of which has since shed some vivid light on the whole subject. Pastor Dzierzon had also clipped the wings of queen-bees, and in thus preventing their nuptial flight and impregnation, observed that the eggs they laid developed only into drones. The facts soon began to be recognised, extended, and thought over by naturalists of the standing of Owen (1843), Von Siebold (1856), and Leuckart (1858), whose conclusions have afforded a firm basis for the abundant subsequent observation and speculation on this interesting subject.

§ 2. *Degrees of Parthenogenesis.*—If we start then with Von Siebold's definition of parthenogenesis, as the power possessed by certain female animals of producing offspring without sexual union with a male, it will clear the ground to notice, in the first place, the numerous different degrees in which this development without fertilisation may occur.

(*a*) *Artificial Parthenogenesis.*—There are a few curious observations which go to show that in exceptional circumstances ova may develop when the male stimulus is replaced by some artificial reagent. These observations must still be taken *cum grano salis*, but they may be at least suggestive of further experiment. Dewitz observed unfertilised frog ova to undergo segmentation (*sic*) in corrosive sublimate solution. In some cases one division occurred, in others several; in some cases irregularly, in others normally. It happened both when the ova were left in the reagent, and when they were merely dipped and returned to water. The eggs experimented on were those of the two common frogs *Rana fusca* and *R. esculenta*, and of the tree-frog (*Hyla arborea*). But it must be noted that Leuckart long ago noted the occurrence of spontaneous division in frog ova. Similarly, Tichomiroff, experimenting with the unfertilised ova of the silkmoth, which are occasionally parthenogenetic, was surprised to observe that ova, which would not of themselves develop parthenogenetically, might be induced to do so by certain stimuli. These consisted in rubbing the unfertilised ova with a brush, or in dipping them for two minutes in sulphuric acid and then washing them. In both cases, he says, a percentage of the ova thus artificially stimulated developed. It must be remembered that occasional parthenogenesis occurs in this insect, and all that Tichomiroff did was to incite this. J. Pérez notes

("P. V. Soc. Sci. Bordeaux," 1896-7, pp. 9-10) that gentle friction of silkmoth eggs stimulates parthenogenetic development, but that it occurs apart from this, especially in the eggs of very robust females. There is no doubt that reagents may considerably modify ova; thus the brothers Hertwig showed how it was in this way possible to overcome the non-receptivity of the ovum to more than one sperm. Nor can one forget how sexual reproduction in parasitic fungi tends to disappear, being possibly replaced by the stimulus afforded from the waste products of the host. In a similar way, the multiplication of cells, so frequently associated in disease with the presence of bacteria, has been referred by more than one pathologist to the "spermatic influence" of these micro-organisms, or of the katastates which they form. The most circumstantial account of successful artificial parthenogenesis is that given by Professor Jacques Loeb, who reared larvæ of a sea-urchin from unfertilised eggs which had been left for a couple of hours in sea-water plus a solution of magnesium chloride, and then returned to the normal medium. Balfour has also cited a remarkable observation of Greeff, who saw unfertilised ova of the common starfish developing in ordinary sea-water, in a perfectly normal fashion, only more slowly than usual.

(*b*) *Pathological Parthenogenesis.*—It has very occasionally been noticed in higher animals, where true parthenogenesis is wholly unknown, that an unfertilised egg starts off on its own resources without any male stimulus whatever. This is noted by Leuckart for frog ova, by Oellacher for hens' eggs, and by Bischoff and Hensen even in mammals.

Barfurth has re-investigated the question of parthenogenesis in the hen's egg, and finds that the segments are non-nucleated, therefore not true cells. He explains the process as wholly physico-chemical. (Versuche über die parthenogenetische Furchung des Hühnereies, "Arch. Entwickelungsmechanik.," vol. ii., 1896.) In the ovarian ova of various mammals, *e.g.* guinea-pig, and rabbit, Janosik has observed (1) regular formation of polar bodies, (2) division into numerous nucleated segments either equal or unequal, (3) fragmentation into many minute parts. (Die Atrophie der Follikel und ein seltsames Verhalten der Eizelle, "Arch. f. Mikr. Anatomie," xlviii., 1896, pp. 169-181, 1 pl.)

Such cases must be regarded as rare abnormalities, comparable perhaps to pathological formations which not unfrequently take place in the ovary, and it is hardly necessary to say that in no case did the development proceed far.

(*c*) *Occasional Parthenogenesis.*—In some of the lower animals, which are not themselves normally parthenogenetic, but have relatives which are, occasional parthenogenesis has been frequently observed. These differ from the above cases, since the results are more successful, often in fact reaching maturity, and also in this, that since related forms are parthenogenetic, the "abnormality" is evidently of a much milder type. The common silkmoth is a good example of this occasional parthenogenesis, which certainly occurs, though rare both in the genus and family. Out of 1,102 unfertilised eggs of the silkmoth, observed by Nussbaum, only 22 developed, and that only up to a certain point. "A whole series of insects," Weismann says, "reproduce exceptionally by parthenogenesis, for instance many butterflies, but that never to the extent that all the eggs which an unfertilised female lays develop, but only a fraction, and usually a very small fraction of the total number, the rest perishing. Examples of successful occasional parthenogenesis (to the extent at least of producing males) are furnished by those worker bees, wasps, and ants which exceptionally become fertile."

(*d*) *Partial Parthenogenesis.*—The queen-bee, as has been already mentioned, is impregnated by a drone in her nuptial flight. The sperms thus received are stored up, and used to fertilise the eggs as she lays them in the cells. Not all the eggs, however, but only those which will produce future queens or else workers. Other eggs, to all appearance similar, are unfertilised, and these, as Dzierzon first clearly showed, develop solely into drones. It is a well-established fact that if fertilisation be prevented by the imperfect development of the wings, or by clipping them, the queen only lays drone eggs. The same happens when she is old and her store of male elements exhausted, or when the sperm receptacle has been removed. Von Siebold carefully examined the eggs from drone-cells, and found that they never contained spermatozoa. Hensen notes an interesting side fact, obviously corroboratory, that "German queen-bees, fertilised by Italian or Cyprian drones, produced hybrid females but pure drones, a proof that on the latter the sperm does not operate." Again, it sometimes happens that what are called "fertile workers" crop up, which in consequence of some accident or misdirected intention in the nutrition, become less abortive than the host of semi-females which make up the body of workers. They are

fertile enough to lay eggs, but their female organs do not seem to admit of their being impregnated. Certain it is that they only produce drones. What has just been said in regard to bees, is also true of some wasps and ants.

(*e*) *Seasonal Parthenogenesis.*—In some of the minute aquatic crustaceans (Cladocera), popularly included under the general title of water-fleas, parthenogenesis only occurs for a season, and is periodically interrupted by the birth of males, and the occurrence of the ordinary sexual reproduction. Males generally reappear in the disadvantageous conditions of autumn, but Weismann denies that there is a direct connection between these facts. The common Aphides are parthenogenetic for a succession of generations, sometimes as many as fourteen, throughout the summer, but the cold and hard times of autumn bring back the males and the sexual process. The fertilised egg lives on through the winter, and develops with the warmth of the next spring. By keeping up the temperature and nutritive optimum for three or four years in the artificial summer of a glass case, Réaumur and Kyber succeeded in rearing as many as fifty continuous parthenogenetic generations. In the gall-wasps (Cynipidæ) there is usually only one parthenogenetic generation between the normal sexual reproductions, but in many insects besides Aphides there are several. It ought to be noted that the parthenogenetic Aphides are hardly at the same structural level as the females which are fertilised; but as the differences mainly lie in the absence of certain accessory genital organs, there is no reason for regarding the parthenogenetic forms, as some have done, as larval.

(*f*) *Juvenile Parthenogenesis.*—Cases do occur, however, where larval forms become precociously reproductive (as sometimes happens among higher organisms), and produce offspring parthenogenetically. Such precocious production of parthenogenetic ova must be distinguished from the entirely asexual reproduction exhibited by many larvæ. No very firm line can indeed be drawn, but in the last cases no cells which can be called ova are present. In 1865 Professor N. Wagner observed what has been much studied since, that in the larvæ of some two-winged or dipterous midges (*e.g.*, *Miastor*), the cells of the reproductive rudiment develop into larvæ within the mother-larva's body. The mother falls a victim to her precocity, for the brood of seven to ten larvæ literally feed upon her to the death. They finally leave the corpse and begin life for themselves,

only, however, themselves to fall victims to a similar fate. The process may thus go on for several generations, during which the ova, or pseudova as some would insist upon calling them, become smaller and smaller. Eventually the larvæ become too constitutionally poor to be precociously parthenogenetic, and develop into adult midges—male and female, the latter producing, however, only a few eggs.

In another dipterous insect known as *Chironomus*, the ova begin to be produced at a very early stage, are laid just at the time when the larval life ends, and develop parthenogenetically. According to Jaworowski, by the rupture of the ovarian membrane the ova fall into the body-cavity, where the abundant nutritive stimulus takes the place of fertilisation. Juvenile parthenogenesis is also said by Von Siebold to occur among the Strepsiptera, little insects which infest bees.

(*g*) *Total Parthenogenesis.*—Lastly, in some of the minute aquatic crustaceans and in many rotifers no males have ever been found. There is every probability that the parthenogenesis is thus total; and as the numbers are abundant, it has apparently been established without detriment to, at least, the continuance of the species.

§ 3. *Occurrence of Parthenogenesis.*—In three distinct sets of animals—rotifers, crustaceans, and insects—parthenogenesis has become a confirmed physiological habit.

(*a*) Take first the curious little rotifers, or wheel-animalcules, which abound both in fresh and salt water. They are usually placed in the chaotic alliance of worm-types, and have long been famous for their alleged power of surviving prolonged desiccation. With one or two exceptions the males are markedly different from the females, and are usually small and degenerate. In one group (Philodinadæ) the females have two ovaries, while males have never been found. They have dwindled out of existence. In the rest the females have one ovary, part of which has degenerated into a yolk-gland, and small males occur. These are quite superfluous as mates, however, for parthenogenesis prevails. Even when impregnation, which is a peculiarly random process, occurs, the sperms appear to miss their mark, and to perish in the body-cavity. The numbers keep up, notwithstanding, so that we have here an entire class where parthenogenesis has firmly established itself.

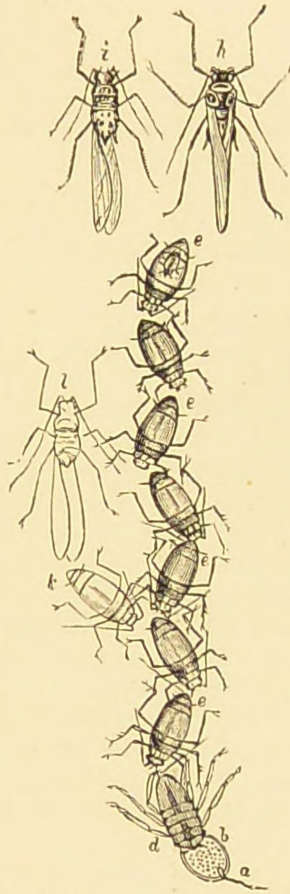
(*b*) Among crustaceans, parthenogenesis is restricted to the lower orders, viz., branchiopods and ostracods. In the former, it is exhibited by the brine-shrimp *Artemia* and the common fresh-water *Apus* in one division; by daphnids (*e.g.*, *Daphnia* and *Moina*, common "water-fleas") in the other. In ostracods, some species of the common *Cypris* are parthenogenetic. If a female water-flea, say *Daphnia*, be isolated from birth, she becomes the mother of an abundant progeny of females. Males and

sexual reproduction do, however, eventually return, and the same is probably true of the majority. Among three thousand specimens of the brine-shrimp only one male occurred; while Von Siebold repeatedly investigated every member of a colony of *Apus*, once over five thousand in number, without finding a single male. At other times he found one per cent., while in certain unknown conditions (probably when food is scarce and life generally unfavourable) the males may be developed in crowds.

In the daphnids, which have been so successfully studied by Weismann, the facts are more complex. There are two kinds of eggs—winter and summer ova. The former are large, thick shelled, capable of resisting drought and the like, and of remaining long latent. They only develop if fertilised, and always produce females. In every way they are highly anabolic ova. The summer eggs, on the other hand, are smaller, and thinner in the shell. They can develop without fertilisation, and that is indeed in some cases physically impossible. Males are produced from summer eggs alone. They usually appear in autumn, when life is becoming harder, or the conditions more katabolic.

In the little cyprids the reproductive relations are very varied. Thus in *Cypris ovum* and *Notodromus monachus* the males are abundant all the year round, and parthenogenesis is unknown. In other species, *e.g.*, *Candona candida*, the males are still frequent, but parthenogenesis nevertheless occurs. Lastly, parthenogenesis prevails in some cases, like *Cypris fusca* and *C. pubera*, and the males are rare, appearing usually in spring.

We may find instances of permanent, seasonal, or even merely local parthenogenesis, —a variety of occurrence which strongly suggests that environmental stimuli are of much importance.



Owen's figure of the Generations of Aphides. At the base an individual arises from a fertilised egg-cell; this gives origin parthenogenetically to a brood, and so on through a succession of generations. At the top the male and female forms reappear, and sexual reproduction returns. At the side an earlier appearance of sexual forms is suggested.

(*c*) In insects, as we have seen, the degrees of parthenogenesis are very varied; so too is the systematic position of the forms in which normal parthenogenesis occurs. Two butterflies (*Psyche helix* and *Solenobia*, 2 sp.) and a beetle (*Gastrophysa*), some coccus-insects and Aphides, certain saw-flies (Tenthredinidæ) and gall-wasps (Cynipidæ), are normally parthenogenetic. In the butterflies just noticed, the males seem to disappear for a stretch of years, and the species gets on without them. The male of *Psyche helix* is very rare, and was for long unknown. When the males are developed in *Solenobia trinquetrella*, it is interesting to notice that they may predominate in numbers over the females. A whole brood may be male; they are brought

back with a rush. About a score of moths, including the silkmoth (*Bombyx mori*) and death's-head (*Sphinx atropos*), have been known to exhibit casual parthenogenesis; but the beetle above noticed stands alone. Bassett, Adler, and others, have demonstrated an interesting alternation of parthenogenesis and ordinary sexual reproduction in numerous gall-wasps. Forms which had been regarded as quite distinct, and had received different generic titles, have been shown in about a score of cases to be merely the parthenogenetic and normal forms of the same insects. From a winter gall the parthenogenetic form emerges which produces a summer gall. In this a sexual form is produced, which eventually gives rise to the winter gall.

§ 4. *Parthenogenesis in Plants.*—The passive bias is so strong in plants, that it is easy to understand the rarity of parthenogenesis. The egg-cell which develops of itself must retain the stimulus which the male element in other cases supplies. It is natural, then, that what predominates in the active rotifers should be uncommon in the sleeping plants. In some of the flowering plants, what looked like parthenogenesis has repeatedly been described, especially in regard to a native of New Holland, known as *Cœlebogyne.* When cultivated in Europe, the male flowers degenerate, and according to Braun and Hanstein disappear. Yet fertile seeds are produced. Karsten found, however, that stamens often persisted; while Strasburger has shown that what developed were not true egg-cells, but adventitious growths from cells outside the embryo-sac. The same is true of some other cases. Dr A. Ernst has recently described what he calls true parthenogenesis in a Menisperm found by him in Caracas, and named *Disciphania Ernstii.* "Female plants, which bore no male flowers, and which were grown perfectly isolated where there was no possibility of the access of pollen from another plant, produced in three successive years an increasing number of fertile fruits."

Kerner von Marilaun and H. O. Juel have shown that in *Antennaria alpina* fertile seeds are produced without impregnation, the male plants being very rare and producing no functional pollen-grains ("Bot. Centralbl.," lxxiv., 1898, pp. 369-372), and there are several similar cases on record.

In the lower plants, however, cases of parthenogenesis abound, apparently as one of the stages in the degeneration of sexual reproduction. It has been casually observed of a species of the stonewort (*Chara*), that when grown in certain waters the male organs disappear, yet the plants continue multiplying. More interesting are the Fungi. To illustrate sexual degeneration, De Bary gives a series from Fungi like those which kill the salmon and potato (Saprolegniæ and Peronosporeæ). What happens first, is the degeneration of the male organs. The katabolic sex from beginning to end is the more unstable. The male function goes first, but the form remains after the reality has ceased. After a while, that is in related species, the form goes too. Sometimes the function is changed, and the male organs become protective sheaths. De Bary's series may be briefly summed up.

(1.) In *Pythium*, the male organ discharges most of its protoplasm into the female,—the usual process.

(2.) In *Phytophthora*, only a very small portion is thus given, and we may almost say asked, for there are curious demand and supply arrangements and compulsions between the male and female organs in these Fungi.

(3.) In *Peronospora*, there is no perceptible passage of protoplasm from male to female, though, without going back to the "aura seminalis," we may allow the possibility of subtle osmosis.
(4.) In some Saprolegniæ, there are indeed the usual antheridia or male organs, which are directed towards the female organs, but do not open. The "explosive" character is diminishing.
(5.) In others, the male organs never get near the female.
(6.) In others, there are no male organs at all, but the female cells develop as usual.

Parthenogenesis is thus reached, as the result plainly of a degenerative process. We can follow the story further, however, forestalling for the moment the subject of the next chapter. The male organ has degenerated, we have seen, while the female organ holds on its course. But this is not always so; in many cases it follows suit, and asexual reproduction remains.

Now why should these Fungi among plants exhibit numerous instances of parthenogenesis? The more intimate the parasitism, the more degenerate the sexual reproduction, and all trace of it is often lost. It may be that in the vital economy of the species the nutritive stimulus of the host in some measure takes the place of fertilisation. Or it may be that the stimuli which Klebs has shown to be operative in inducing the occurrence of asexual or sexual reproduction in Algæ and Fungi which have both modes of multiplication, are absent in the parasitic forms above referred to.

Male parthenogenesis, paradoxical as it sounds, is really exhibited among lowly Algæ. That is to say, a small spore (or male-cell) which normally unites with a larger and more quiescent one (or female-cell), may occasionally start developing on its own resources. The result, however, is poor enough. As those spores are on the border line between asexuality and differentiated sex-elements, the retention of a vegetative power of division even by the incipient male-cell is not surprising. Nor must it be forgotten that the mother-sperm-cell itself has a power of parthenogenetic development. It divides, like its homologue the ovum, into a ball of cells, but, having none of the conservative coherence of the latter, breaks up into spermatozoa. It is exactly comparable to the interesting Protozoon (*Magosphæra*) which Haeckel saw, which did its best to get beyond the Protozoa, but failed as soon as it had succeeded. A single infusorian-like cell divided into a ball of cells, but the ball had no coherence and broke up into infusorians once more.

§ 5. *The Offspring of Parthenogenesis.*—The fate of parthenogenetic ova is very diverse. They may all perish, or all succeed; they may turn out wholly males or wholly females. Hensen notes the following suggestive series, with decreasing reproductive, as opposed to constitutional, energy at each level:—

(1.) Hermaphrodites, then only females.
(2.) Series of females, then mixed brood.
(3.) Several females, mixed brood, then only males.
(4.) Series of mixed broods, then males, or death of ova.
(5.) Mixed brood, with much mortality.
(6.) Males only.
(7.) Development only for a few stages.

Rolph has a different arrangement, but the same idea:—

(1.) Exceptional parthenogenesis with uncertain result (*e.g.*, Silkmoth).

(2.) Normal, producing males only (female solely from fertilised ova) (*e.g.*, Bees).
(3.) Mostly males, with occasional females (*e.g.*, *Nematus*).
(4.) Mostly females, with exceptional or periodic males (*e.g.*, *Apus*, *Artemia*).
(5.) Only female, males unknown (*e.g.*, many Rotifers).

That parthenogenetic ova should develop with such diverse results is not at all surprising. The absence of fertilisation removes one of the factors determining sex; but food, temperature, age of ovum, &c., remain, and produce bias now to one side, now to the other. To this we shall presently return; meanwhile the facts of offspring may be more clearly expressed thus:—

	Result.	Example.
Parthenogenetic Ovum.	*Nil*	Most organisms.
	Partial and pathological development .	Rarities mentioned.
	Great mortality in a mixed brood. . .	Many insects.
	♂'s alone	Hive-bee and some other forms.
	♂'s mostly, a few ♀'s	*Nematus* (allied to bee).
	♂'s and ♀'s (one generation) . .	Most gall-wasps.
	♂'s, and more than a few ♀'s . .	Some saw-flies.
	♀ ♀ ♀ (a succession), then a predominance of ♂'s	Some water-fleas.
	♀ ♀ ♀, then equal numbers of ♂'s and ♀'s	*Solenobia* sometimes.
	♀ ♀ ♀, then a minority of ♂'s among ♀'s	Aphides; some water-fleas.
	♀ ♀ ♀ ♀, very rare ♂'s . . .	Many water-fleas.
	♀ ♀ ♀ ♀, non-functional ♂'s among ♀'s	Most rotifers.
	♀ ♀ ♀ ♀, ad infinitum, no ♂'s . .	Many rotifers.

§ 6. *Effects of Parthenogenesis.*—Since parthenogenesis is dominant in rotifers, and well established among water-fleas and plant-lice, it is very plain that whatever else it affects, it is anything but prejudicial to numbers. An aphis will continue for days producing a viviparous brood, at the rate of one per hour; the offspring soon begin themselves to multiply; and Huxley calculates that if this continued for a year without mortality, a single aphis would be the ancestor of a progeny which would weigh down five hundred millions of stout men! Not gardeners only have cause for gratitude that climate and enemies prevent such untoward increase. But there are other desiderata besides numbers. Can it be said that parthenogenesis favours the general life and progress of the species? More than one of the old naturalists, and in recent years Brooks, Galton, Weismann, and others, have laid emphasis on the value of fertilisation as a fountain of change. To Weismann

the intermingling of the male and female "germ-plasms" in fertilisation is one of the possible sources of variation. If it be removed therefore, as in rotifers, the species will be so much the less likely to progress, the establishment of parthenogenesis will be a handicapping of evolution.

But Weismann has shown that variation still occurs in the parthenogenetic Cyprids, and variations of Rotifers, *e.g.*, *Anuræa cochlearis*, have been often recorded. In the well-known case just mentioned, however, the varieties are correlated with the seasons, and it seems to us probable that they are seasonal "modifications" rather than true constitutional variations.

While recognising, then, the occurrence of variations in forms where the reproduction is parthenogenetic, or even quite asexual, we suggest the probability that the absence of fertilisation involves some diminution in the frequency and range of variability.

§ 7. *Peculiarity of the Parthenogenetic Ova.*—Before a theory of parthenogenesis is sought, the natural question arises, Are these eggs that develop of themselves in any way peculiar? (*a*) For a while it was supposed (*e.g.*, by Balfour) that parthenogenetic ova did not form polar globules, and the theory based upon this regarded the retention of these bodies as taking the place of fertilisation. The demonstrated occurrence of one polar globule in several parthenogenetic eggs partially demolished this theory, and it is only within the last two or three years that it has been restated in accurate form. (*b*) Simon shrewdly points out, that in some of the most marked cases of parthenogenesis the sex-cells are insulated from the body at a very early stage. This is notably so in those midges which reproduce parthenogenetically even before maturity. It is certainly striking that these forms should unite an extreme earliness in the embryonic separation of the germ-cells with a most precocious reproduction. These germ-cells are ova which have a much less circuitous history than in most cases; they have far fewer cell-divisions behind them, they have thus a reserve power of division which other ova have not; they are able, in fact, to develop of themselves. Although this is not known to be true of all instances of normal parthenogenesis (*e.g.*, rotifers), it is true of some, and that to a greater extent than was known when Simon wrote. On the other hand, some forms where parthenogenesis is

unknown (*e.g.*, leeches and *Sagitta*), also exhibit the same early differentiation of germ-cells, so that we can only look upon the fact as one of the auxiliaries of parthenogenesis

(*c*) The peculiarity of parthenogenetic ova, which has of late attracted much attention, is that they extrude only one polar cell,—not two, like other eggs. Weismann, with the assistance of Ischikawa, proved this for the parthenogenetic ova of Rotifers and Ostracods, such as *Polyphemus*, *Leptodora hyalina*, *Sida crystallina*, *Cypris reptans*. Blochmann has also corroborated Weismann's discovery by observations on aphides, but he found *two* polar bodies in those unfertilised eggs of bees which give rise to drones. The occurrence of two polar bodies was also noted by Platner in the parthenogenetic ova of a butterfly (*Liparis*). The apparent contradiction has been in part explained by the discovery of Brauer that in the parthenogenetic ova of the brine-shrimp *Artemia*, two modes of maturation occur. In most cases only one polar body is formed, in other cases two are formed, but the second does not leave the egg and behaves just like a sperm-nucleus. A further enquiry into the exact history of the nuclear rods or chromosomes shows that the two cases can be plausibly reconciled.

§ 8. *Theory of Parthenogenesis.*—(*a*) We may begin with Balfour's view of the case, though that of Minot has the priority. "The function of forming polar cells has been acquired by the ovum for the express purpose of preventing parthenogenesis." If they were not formed, parthenogenesis would normally occur. This is expressed in curiously teleological language, but the main idea is clear enough,—the retained polar cells replace the sperm nucleus.

(*b*) "In accordance with Minot's hypothesis of sexuality, it might be assumed that in parthenogenetic ova the male element was retained, and that the cell remained a true asexual cell, and did not become a sexual element." "Blochmann and Weismann have shown that this is the case, by their discovery that in parthenogenetic ova only one polar globule is formed, while there are always two in ova which are impregnated; hence it is probable that one polar globule (by hypothesis, male) is retained."

Minot's words are not beyond criticism either, though they are not teleological. An ovum which retains a male element is not happily described as remaining asexual; it would be better to call it a case of intra-cellular hermaphroditism. It is

more important, however, to notice how Minot cleverly adapts his theory to increased knowledge of the facts. The parthenogenetic ovum only retains one polar globule,—one male element is enough; two would be "polyspermy," which is abhorred.

(*c*) There was no fear that Rolph would indulge in teleology, rigid necessitarian as he was. Parthenogenesis of ova was to him the more natural process, the sperm a subsequent importation. "There is for the ovum a certain minimal mass, which must be surpassed if it is to develop at all; and a second minimum, which the ovum must attain, if a female is to be produced." Abundant nutrition of the ovum tends to parthenogenesis, producing male offspring, as the lower stage; but if the second limit be attained, resulting in females. In the opposite direction, if the ovum has fewer resources, it requires to be fertilised. Females or males will again result according to the state of the elements. If no fertilisation occur, the dependent ovum must of course die. Rolph is always suggestive, but he erred in regarding the sex-elements too quantitatively, in missing the qualitative antithesis of sex, and the opposition observed in cell-division.

(*d*) Strasburger also lays emphasis, in a subtler and more technical way, on nutritive conditions. "In the rare cases of parthenogenesis, specially favourable nutritive conditions may counteract the lack of nuclear plasma." He notes three different ways in which this may happen, and also inclines to believe that retention of polar globules would favour parthenogenetic development. It is important to notice how two naturalists, so very different in their manner of attacking a subject as Rolph and Strasburger are, come to this conclusion at least in common, that favourable nutritive conditions favour parthenogenesis. All the cells in the body tend to multiply, the ova retaining this power develop embryos.

(*e*) Weismann has a peculiar right to be heard on the nature of parthenogenesis; for not only has he been for many years an investigator of the tiny daphnids or water-fleas, but he made the important discovery, already noticed, that parthenogenetic ova extrude only one polar globule. There has not been time yet to prove that this is always true, but the probabilities are strong that it is. Weismann's first supposition was that in maturation of ordinary ova the first polar division got rid of "oogenetic" nuclear plasm, and that the second removed part of the essential germ-plasm; and that in the maturation of par-

thenogenetic ova only the first process occurred. This view is expressed in the following paragraphs.

"Parthenogenesis occurs when the entire sum of the ancestral elements persists in the nucleus of the ovum. Development by fertilisation demands, however, that half of these ancestral elements must first be extruded from the ovum, whereupon the remaining half, in uniting with the sperm nucleus, regains the original number.

"In both cases the beginning of development depends upon the presence of a definite, and indeed similar mass of germ-plasma. In the ovum which requires fertilisation, this is afforded by the importation of the sperm-nucleus, and development follows on the heels of fertilisation. The parthenogenetic ovum already contains the necessary mass of germ-plasma, and this becomes active as soon as the single polar body has freed the ovum from the oogenetic nuclear-plasma."

He has now given up the hypothesis that the first polar body removes "oogenetic idioplasm," and the second germ-plasm; he admits that germ-plasm is got rid of in both cases. In parthenogenetic ova, however, where only one polar body is extruded, a sufficient quantity of germ-plasm is retained to make development without fertilisation possible.

The view which Weismann now holds (*vide* "The Germ-Plasm," 1893) seems to amount to this, that the reduction of germ-plasm in the maturation of ordinary ova is too great to admit of independent development, but that in parthenogenetic ova the reduction is less and development without fertilisation occurs. It may be urged that we have not as yet sufficiently secure data in regard to the reducing processes in parthenogenetic ova, and it must be noted that there are some authorities who refuse to grant that the emphasis which Weismann and others have laid on the reducing divisions is justified. Thus Professor Hartog maintains ("Natural Science," xiii., 1898, pp. 115-120) that the process of nuclear reduction does not affect the quantity of nuclear material, but only the number of segments into which it is divided. He suggests that it is the achromatic plasma or linin which bears the hereditary characters, and that the chromatin has only a mechanical function.

Weismann's pre-occupation with questions of inheritance has given a bias to his theory, making it morphological rather than physiological. A given quantum of germ-plasma, he says, fits the ovum to develop. The parthenogenetic ovum keeps enough. The ordinary ovum extrudes so much that it has to get it back again from another source. It appears to us more in accordance with the facts to suppose that the entrance of the sperm has a twofold importance,—(*a*) It bears with it certain hereditary characteristics, doubtless in the nucleus for the most part; (*b*) it brings with it a stimulus to division of a qualitative character, doubtless in some part in its small cell-substance. This last function—the dynamic function—Weismann wholly denies. The sperm has to him only a quantitative function.

(*f*) Our theory of parthenogenesis may now be stated. Just as the spores which illustrate the beginnings of sex may sometimes dispense with conjugation and germinate independently, so may ova develop parthenogenetically. These are to be regarded as incompletely differentiated female cells, which

retain a measure of katabolic (relatively male) products, and thus do not need fertilisation. Such a successful balance between anabolism and katabolism is indeed the ideal of all organic life. In parasitic fungi, sexual reproduction disappears, and surrounding waste products presumably help the purpose otherwise effected by sexual organs, so peculiarities in the conditions of parthenogenetic ova may explain the retention of the normal balance which makes division possible without the usual stimulus of fertilisation. Abundant and at the same time stimulating nutrition (Rolph), early differentiation of the sex-cells (Simon), the general preponderance of reproductive over vegetative constitution (Hensen), their liberation before the anabolic bias has carried them too far, are among these

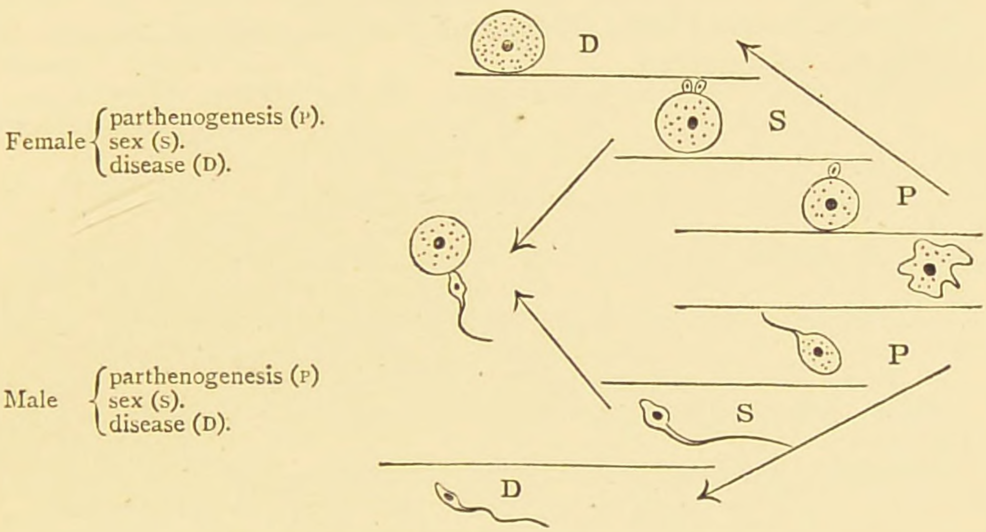


Diagram illustrating the theory of parthenogenesis.

favouring conditions. Artificial parthenogenesis can be induced in some cases by chemical reagents; thus in Loeb's experiments with sea-urchin ova magnesium chloride seemed to have (perhaps very indirectly) the same physiological rôle as spermatozoa. The incipient segmentation observed in a few ova is an independent effort to save themselves from being too big to live, since they are not passive enough to remain dormant. Waste has set in, self-digestion begins, the cell is forced into the expedient of division. In higher animals this is all in vain: in lower animals such imperfectly differentiated female cells are commoner; they form the parthenogenetic ova.

§ 9. *Origin of Parthenogenesis.*—From the occurrence of parthenogenesis in the animal series, it is certain that it has

originated as a degeneration from the ordinary sexual process. It is no direct persistence of a primitive ideal state, though in a sense a return to it.

It seems to us misleading to interpret the occurrence of parthenogenesis as due to "motives" and "important advantages." These are afterthoughts of our importation. It is not easy indeed to keep from metaphorical language which suggests that polar globule-formation is a "contrivance," and parthenogenesis a "device." Such casual words are of little account; but it is going far to say, as Weismann does, "that sexual reproduction has here been given up, not by any chance nor from internal conditions, but from quite definite external grounds of utility (Zweckmässigkeitsgrunden)." Our position is the converse, that parthenogenesis arises because of necessary internal conditions, and may be perpetuated because of certain advantages.

SUMMARY.

1. Parthenogenesis was formerly believed to be of wider occurrence than it really is, but it is definitely known to be not uncommon in lower animals.

2. Artificial, pathological, occasional, partial, seasonal, juvenile, and total parthenogenesis must be distinguished.

3. The occurrence of parthenogenesis is especially well seen in rotifers, crustaceans, and insects.

4. It is rare among plants, but certainly occurs in some.

5. The offspring of parthenogenetic ova are very diverse.

6. The effects of parthenogenesis on the species deserve consideration, especially by those who find in sexual intermingling an important source of specific variation.

7. So far as we know, parthenogenetic ova (with two or three exceptions) form only one polar body.

8. Parthenogenetic ova are here regarded as imperfectly differentiated female cells, retaining certain characteristics which compensate for the absence of fertilisation.

9. In origin parthenogenesis is regarded as a degeneration from the ordinary sexual process.

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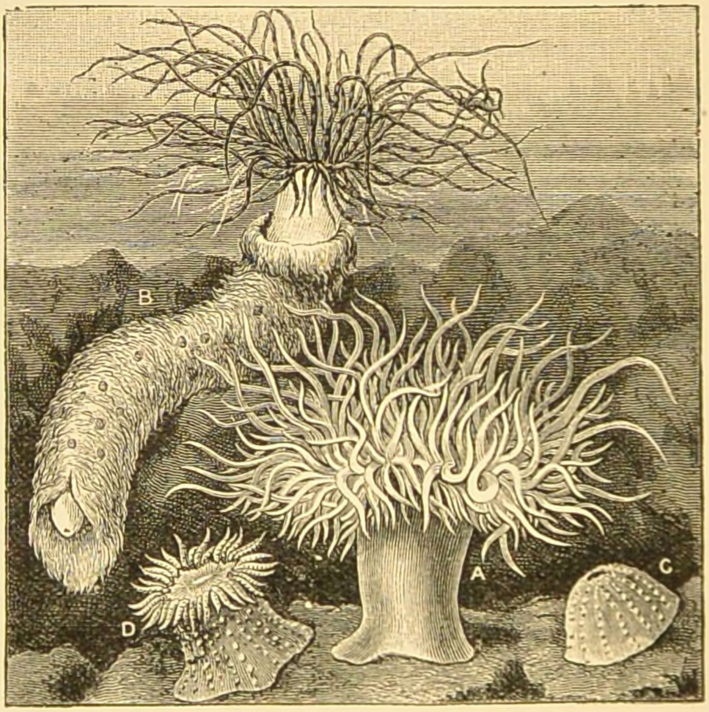
CHAPTER XIV.

ASEXUAL REPRODUCTION.

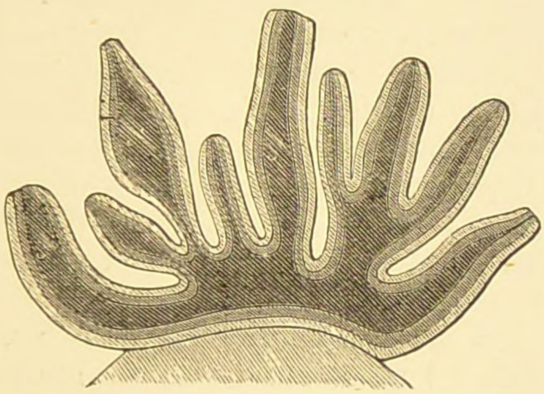
§ 1. *Artificial Division.*—Weeping willows are by no means scarce trees in Britain, yet, as they never flower, they must all have grown from slips. In other words, their multiplication is asexual and artificial. So too, only more naturally, the Canadian pond-weed (*Anacharis*) has spread prodigiously in



A group of Sea-Anemones.—From Andres.

our lochs, canals, and rivers, never bearing male flowers, but owing its increase wholly to the asexual process. Every one knows how the gardener increases his stock by slips and cuttings, thus taking advantage of the power a part has to reproduce the whole. Bananas, potatoes, and yams are in the same way propagated asexually, and this is also the usual

method in the case of olives, figs, and date palms. Quite in the same way, cultivators of bath sponges are able to bed out little fragments. In the last century, the Abbé Trembley delighted himself and others by the now familiar observation, that to get many hydra polypes, the simplest and quickest way was to cut one in pieces. A fragment will reproduce the whole, provided always that it have to start with fair samples of the different kinds of cells in the body, and that it be not too minute. The same may be done with the much larger sea-anemones. So the earthworm, curtailed by the spade, does not necessarily suffer loss, though it may suffer pain. The head portion grows a new tail, and even a decapitated portion may



The Formation of a Sponge Colony (*Olynthus*) by budding.—After Haeckel.

reproduce a head and brain, not that this is saying much for these.

§ 2. *Regeneration.* — Spades and knives are not exactly instruments of nature, but they have their counterparts. Fighting with a rival a crab may lose its claw, or the same may happen in the frequently fatal moulting. Slowly, however, the loss is made good; the cells of the stump multiply, and arrange themselves in obedience to the same necessities as before, and a limb is regenerated. Many an appendage among the lower animals is from time to time nipped off, only to be grown again. A snail has been known to regenerate an amputated eye-bearing horn twenty times. A starfish readily surrenders an arm, and a lizard its tail. Indeed, many animals may be said to have learnt organically, though not consciously, that it is better for one member to perish than for the whole life to

be lost. For animals, like men, are often wiser than they wot of. In the panic of capture, strong convulsions may occur; thus the sea-cucumber may surprise and perhaps shock its persecutor by the ejection of its viscera; or a tetanic contraction of the muscles makes the slow-worm brittle in the hands of its captor. The power of regeneration is most marked in echinoderms, but persists as high up as reptiles. The re-growth of part of a lizard's leg is the *chef-d'œuvre* in this line. Beyond that, regeneration is restricted to little things. We constantly regenerate the skin of our lips, but we cannot naturally replace an amputated limb.

The regenerative capacity depends on primary properties of the living matter and of the organism—which we are far from understanding,—but it seems probable, as Réaumur, Lessona, Darwin, Weismann, and others have pointed out, that its distribution and mode of occurrence are adaptive, being related to the normal risks of life. According to Lessona's law, which Weismann has elaborated, regeneration occurs in those organisms and in those parts of organisms which are in the course of nature most liable to injury. (See Weismann, "Natural Science," xiv., 1899, pp. 305-328; "Anat. Anzeiger," xv., 1899, pp. 445-474.)

This position may be argued for in two ways. One may try to show that all parts known to be markedly capable of regeneration are liable to be lost or injured under natural conditions; and one may show that parts not very liable to be injured are not regenerated, although they are often of great importance.

It must be admitted that there are cases of regeneration—*e.g.*, of a stork's bill or a newt's eye—where the natural liability to injury is not at first sight evident. But inquiry shows that male storks fight savagely, and that the head, and possibly the eye of the newt, are often attacked by the larvæ of the water-beetle (*Dytiscus marginalis*). But an explanation of the regenerative capacity of the protected abdominal limbs of hermit-crabs, which T. H. Morgan has demonstrated, is more difficult, unless one supposes that the power has been inherited from ancestral Crustaceans whose abdomen was unprotected, or that the liability to injury to which the supposed adaptation is related is associated with the process of moulting. That the latter supposition should be tested is made clear by the observations of Bordage on Phasmids and other Orthoptera.

But Morgan's criticism of Weismann's position has not yet been adequately met.

As to the second point, it will be admitted by most that injuries to internal organs are seldom made good.

§ 3. *Degrees of Asexual Reproduction.*—The keynote of the subject was struck by Spencer and Haeckel, when they defined asexual reproduction as discontinuous growth. All growth is a reproduction of the protoplasm and its nuclear elements, or, in short, of the cells; all reproduction (excluding the important event of fertilisation) is growth. The ovum, asexually produced from the parent ovum or its lineally descendant cells, grows and reproduces itself in turn, building up the embryo. The embryo grows into an adult organism, and the surplus of continued growing energy results in the asexual production of buds, or the sexual discharge of differentiated reproductive elements. We may start from the ordinary processes of cell-multiplication and regeneration exhibited in the normal organism. Then come the processes by which lost members are regenerated, involving more or less serious extra growth. From these we may pass to the rarer and yet not rare cases, where the artificial halves or fractions of an organism can grow into wholes. Normal and frequent, however, are the very abundant cases of budding, where a sponge or hydra, zoophyte or coral, has surplus enough to grow off new individuals, which remain continuous with itself. The parent organism, whether zoophyte or strawberry-plant, has an asexually produced progeny round about, and in asexual continuity with itself. But they do not always remain continuous; the hydra produces buds, but eventually sets them adrift. This is still better seen in many of the hydroids, where individuals are separated off as swimming-bells or medusoids. The multiplication has become discontinuous. Continue the process, and we find the liberation of special cells, clinging often for a time to the parent, generally dependent for development on union with similar cells of complementary constitution; we find, in fact, the sexual reproduction which, in the higher organisms, so thoroughly replaces the asexual process.

§ 4. *Occurrence of Asexual Reproduction in Plants and Animals.*—In plants, as one would expect from their vegetative constitution, the asexual process is common, particularly among the lower forms. The common liverworts (*Marchantia* and *Lunularia*), through the formation of asexual buds or gemmæ

in the cups upon their thallus, rapidly overrun our flower-pots, and become a pest of the greenhouse. Many ferns too, notably among the Aspleniums, reproduce by bulbils, arising upon the frond; and the bulbils which arise in the axils of the leaves of the tiger-lily are familiar missiles for every child accustomed to a flower-garden (see figs. pp. 211 and 240). The Alliums, and some of our common grasses also, furnish us with examples of the replacement of flowers by separable buds. Asexual reproduction, or multiplication by more or less discontinuous

Asexual Propagation of a Grass—(*a*) the bulbils rooting on the ground; (*b*) their appearance in the inflorescence; (*c*) a small portion enlarged.—From nature.

growth, without the differentiation of special and mutually dependent sex-cells, occurs from the simplest animals on to the tunicates or sea-squirts, from the base to just over the line which separates backboneless and backboned animals. It is necessary, however, to review the groups.

Protozoa.—Fertilisation began in almost mechanical fusion. Reproduction begins with almost mechanical rupture. The unit mass of protoplasm, becoming too big for control, breaks. Thus it saves itself, and at the same time multiplies. Such breakage may be seen in some primitive amœboid

forms, but it also occurs in a few of the relatively high infusorians. That the breakage sometimes means dissolution is certain; nor is reproduction ever so very far removed from death.

The rupture becomes orderly and systematic in budding. This may be multiple, as in the common *Arcella*, where a number of small buds are constricted off all round. But the process is oftener concentrated in one extrusion or overflow. In budding, the separated daughter-cell is in varying degree smaller than the parent, and the process resembles an overflow. When the bud is approximately equal to the parent, and the process is of the nature of a constriction, it is, of course, division.

The division may also be multiple, taking place in rapid succession and in limited space, *e.g.*, within a cyst. Then we speak of spore-formation. The last three modes of multiplication are exceedingly common among Protozoa.

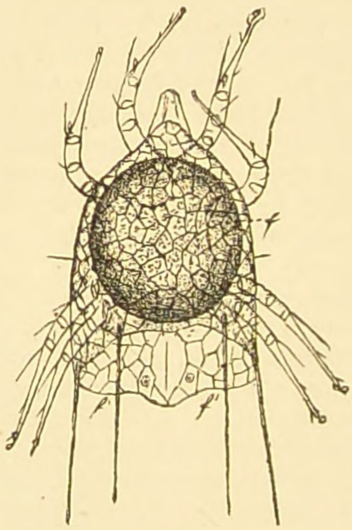
These buddings and divisions are not, of course, rough and ready processes. The nucleus almost always shares in them in an orderly and complicated fashion. There are variations in its behaviour as in higher animals, but there is no doubt that cell-division, with a gradient of progress like everything else, is essentially one and the same in the vast majority of cases. Gruber has been especially successful in proving that fragments of Protozoa, artificially separated without nuclear elements, cannot live long. Though they may retain for a time contractility and irritability, they cannot feed or grow. The nucleus is essential to life, though sometimes it seems to disappear, and become as it were a diffuse precipitate in the protoplasm.

Sponges.—In sponges no one can fail to recognise the impossibility of drawing any rigid line between growth and asexual reproduction. Between simple extension of the parent mass, and the budding off of new individuals, no sure distinction can in many cases be made out. Sponges do not divide, though they may be cut up, yet some give off discontinuous buds. An outgrown tube may lose connection with the parent, or a great tumour-like mass may be slowly extruded, or tiny brood-buds may be set adrift to shift for themselves. In disadvantageous conditions the surface of a sponge sometimes gathers into minute superficial buds, by means of which it is possible that the life is saved.

In the fresh-water sponges, in disadvantageous circumstances,—of cold in some countries, heat and drought in others,—some of the cells club together to form gemmules, which often save the life of the otherwise dying sponge. They are complex enough, with sheaths and spicules, and sometimes even with a float, but in principle they simply do by a multiple union what is otherwise attained by ovum and sperm. Best known in this respect is the freshwater sponge (*Spongilla*); but gemmules have also been described in other common sponges, *e.g.*, in *Cliona*, the borer in oyster shells.

Cœlenterates.—In such names as zoophytes, sea-firs, sea-roses, there is a suggestion of the undoubtedly plant-like character of many of the cœlenterates. A sessile habit is very general, though often only a phase in the life-history, and asexual reproduction runs riot. A well-fed hydra is prolific in bud-bearing; and numerous gradations connect this with the myriad colonies exhibited by many hydroids. The individuals forming a united family share in the common life and nutriment. As the colony becomes complex, it is often physically impossible for all the members to

remain on terms of even approximate equality of internal and external conditions. One becomes relatively overfed, another starved. Slight differences of function gradually become emphasised and exaggerated, till division of labour is established. The structural aspect of this is differentiation or polymorphism among the members of the colony, and results in the establishment of nutritive and reproductive, sensitive and protective, "persons." Thus in the common *Hydractinia*, the open-mouthed nutritive individuals are markedly contrasted with the dependent reproductive persons; and again, in different form, the rhythm repeats itself in the contrast between active, offensive, and sensitive elongated members, and entirely passive and abortive spines, which form a chevaux-de-frise under shelter of which the others cower. It is usually supposed that the sessile hydroids are in a sense degenerate from more active ancestral types. The free-swimming embryo becomes exhausted, settles down, and exhibits predominant vegetativeness with postponed sexuality. In many cases, how-



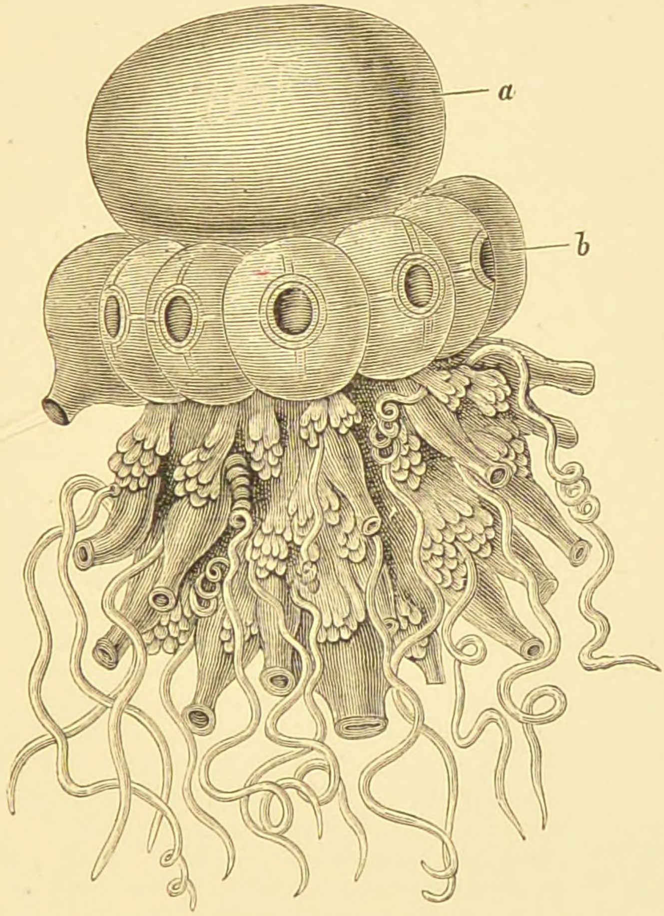
One of the acarids or lice (*Glyciphagus cursor*) forming a life-saving cyst, while the individual itself dies.

ever, there is a recovery of the ancestral liberty of action, for modified "persons" are set adrift as active, free-swimming, sexual medusoids.

There are, however, active forms of the true medusoid type (Trachymedusæ) which never descend to the sessile nadir of existence, but yet exhibit the asexual tendency of the class in forming temporary clusters of pendent buds. Lang has described a remarkable compound medusoid (*Gastroblasta raffaelii*), which has sometimes as many as nine stomachs, and may be assumed to be highly nutritive. The remarkable point, however, is that the compound adult is the result not only of continued budding, but of a process of rectangular incomplete division. Along with some others it leads on towards the Portuguese man-of-war, or siphonophore series. Here the larva develops at first into a simple medusa-like individual, but this buds off a manifold series of "persons," which, by dislocation or even migration, become arranged in all the beauty of the siphonophore colonies, which surpass even *Hydractinia* in their division of labour. It is difficult enough in some cases to distinguish between true

"persons"—which Haeckel calls "Medusomes"—and mere organs like protective bracts, which are also budded off.

In another direction, viz., among the true jelly-fishes (Acraspeda), where an active habit greatly preponderates, we still find the occurrence of asexual multiplication. Some forms (*e.g.*, *Pelagia*) are entirely free; at the opposite extreme a few (*Lucernaria*) may be described as sedentary; between these we find the common *Aurelia*, which settles down in its youth, and gives rise by division to what afterwards become the large sexual jelly-fishes (see fig. p. 215).

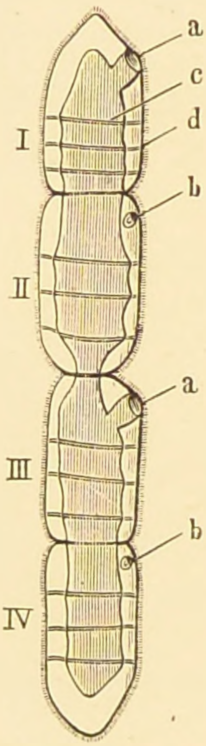


Siphonophore Colony, showing the float (*a*), the swimming-bells (*b*), and the nutritive, reproductive, and other "persons" beneath.—From Lang, after Haeckel.

There remain two classes of cœlenterates,—the Ctenophora, like *Beroe*, which represent a climax of activity, and never divide; and the Actinozoa (sea-anemones and corals), which lead to a passive terminus again, and exhibit profuse asexual multiplication. A few sea-anemones divide normally, just as they may be multiplied by artificial cutting. Fragments may also be given off in an arbitrary sort of fashion, reminding one of the overflow buds of sponges. In *Metridium fimbriatum*, studied by H. B. Torrey ("Proc. California Acad. Sci.," 3rd Series, i., 1898, pp. 345-360, 1 pl.),

there is a great variety of asexual multiplication, which may occur by longitudinal fission, laceration, and budding. The budding of corals takes many forms, resulting in the quaint complexity of brain-corals and the like. In one sea-anemone (*Gonactinia prolifera*), where transverse division occurs, it is interesting to notice that this has only been observed in young forms with undeveloped sexual organs. It recalled, in fact, the asexual multiplication of a young jelly-fish. In another of the corals (one of the Antipatharia) Brook observed that a nutritive "person" may, by constriction, form a reproductive individual on either side.

Worms.—The lower worm-types are roughly distinguishable from most of the higher by the broad fact that they are all of a piece, without rings or segments. A physiological link, however, between worms of only one segment and those with many, is found in the asexual chains which some of the former occasionally develop. Thus the little turbellarian *Microstomum lineare* may bud off a temporary chain of sixteen individual links. The budding begins at the posterior end, and what is partly separated off is a portion in excess of the normal size. The second link grows till it attains the usual adult size, and as it exceeds this forms a third link. At the same time the original individual may also be doing the same, and thus a chain of four is formed. Two more buddings by each of the links bring the asexual process to a climax, and then the individuals separate from one another and become sexual in freedom. It is important to notice that the asexual reproduction takes place in favourable nutritive conditions, and as each individual exceeds its normal limit of growth. In some allied planarians the asexual multiplication is effected not by budding but by division. Zacharias observed that when nutrition was checked the vegetative increase ceased, and sexual reproduction set in. Not quite parallel with the above, but quite asexual, is the prolific multiplication characteristic of the flukes and tapeworms. The common liver-fluke has several asexual generations before it finds its final host in the sheep, and is surpassed in this respect by some of its relatives. A bladder-worm, in passive ease, with a plethora of nutrition, may form asexually many "heads," each of which, inside a future host, grows out into the long series of joints which compose the tapeworm. In their profuse asexual multiplication these parasites are like parasitic fungi, but unlike them in the retention of the sexual process as well.

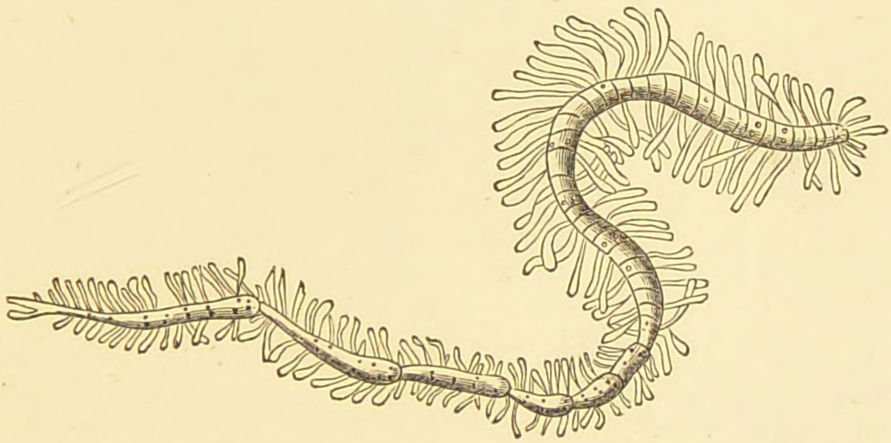


Diagrammatic representation of the formation of a chain of individuals in the Turbellarian worm *Microstomum lineare.*—From Leunis.

In their asexual reproduction, the Polyzoa recall sponges, for not only do they all multiply by budding, and that abundantly, but they form peculiar winter-buds like sponge-gemmules, by which, on the death of the parent, the continuity of life is nevertheless sustained. The winter-buds or statoblasts may further resemble sponge-gemmules in elaborateness of external equipment, a common characteristic of passive resting structures.

In the higher bristle-footed worm-types (Chætopoda), asexual multiplica-

tion occurs in great variety of expression. Some, when alarmed, break up into pieces, and others are known to do this in apparently normal life. Each part in favourable conditions may reproduce the whole. Thus, at a comparatively high level among animals, reproduction may be literally rupture. Oftener, however, budding precedes the division, and curious chains of ringed worms are thus produced. Nor do the budded individuals always keep in a straight line, but, as in the freshwater naids, may abut at angles, and form a quaint living branch. To what degrees this irregularity of budding may attain is well seen in the accompanying cut of a portion of a worm (*Syllis ramosa*), found on the "Challenger" voyage. The buds occur laterally, terminally, or on any broken surface, and the result is an almost bush-like compound organism rivalling even the hydroids in the freedom of its branching. Some of the branches become males or females, and go separate, or are sent adrift. In other syllids the separation of a series of joints as a sexual individual has been repeatedly observed, or this may be reduced till only one joint, laden with reproductive elements, is set

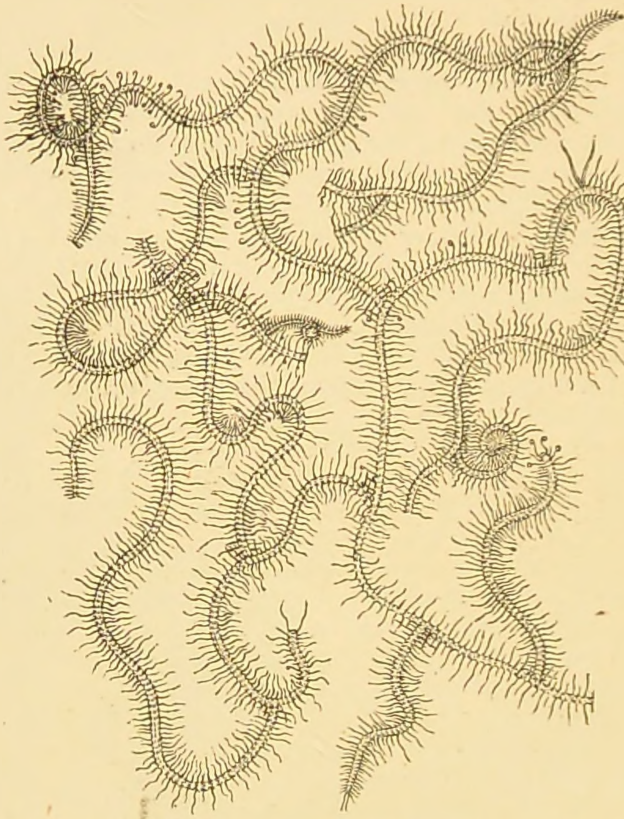


A Sea-worm (*Myrianida*) which has budded off a chain of individuals.—After Milne-Edwards.

free. In many of the Chætopods the budding begins when the normal size of the individual has been stopped by unfavourable conditions, which bring about separation, and the subsequent sexuality of the liberated individuals. When the entire individual is modified at the sexual period the term *epigamy* is used; this is illustrated among Nereidæ, Syllideæ, and Hesioniæ. When only a part is modified sexually and is discharged as a mouthless free-swimming form, the term schizogamy is used. This is best known in various species of *Syllis*. In some cases, however, *Exogone gemmifera* and *Autolytus longeferiens*, both epigamy and schizogamy are illustrated in one life-cycle. (See A. Malaquin, "Epigamie et Schizogamie chez les Annélides," *Zool. Anzeig.*, xix. (1896), pp. 420-423.) The facts in regard to reproductive processes in these Polychaet worms are indeed very complex; we cannot do more than note three representative modes.

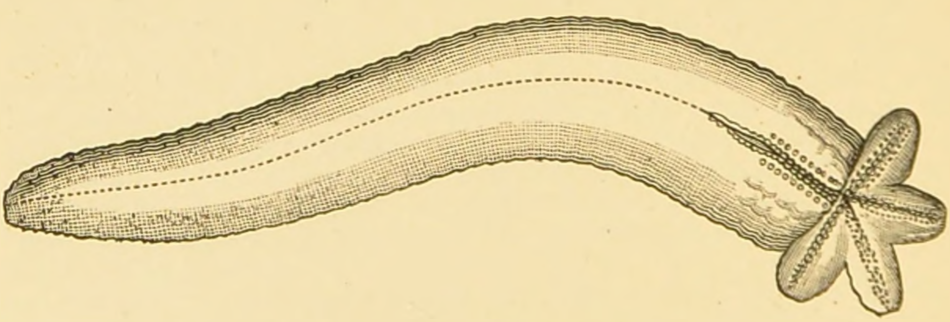
(*a*) In *Nereis*, for instance, certain of the segments become sexually mature (epitokous) and differ markedly from the non-reproductive (atokous) segments; but reproduction (usually fatal) occurs without any separation of the epitokous and atokous parts.

(*b*) In the palolo-worm, *Eunice viridis*, portions of which swarm in extraordinary numbers at certain definite times off Samoa, about two-thirds



Syllis ramosa, a ringed marine worm, in which asexual multiplication has produced a branched appearance.—From M'Intosh, "Challenger" Rep. on Annelida.

of the body is reproductive or epitokous, and differs in its narrowness, dark colour, and structural details from the anterior atokous region. The epito-



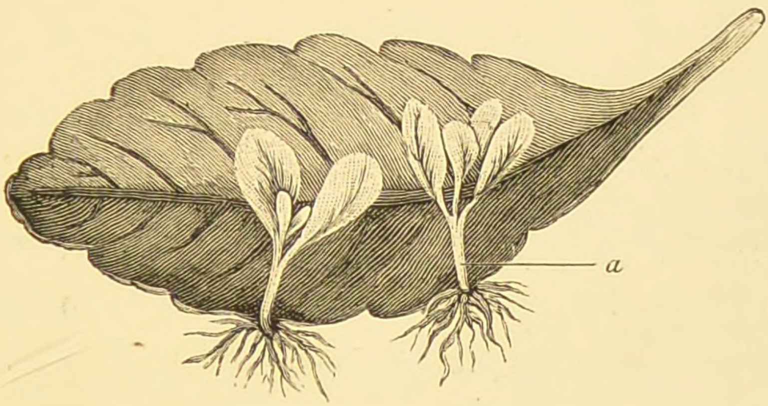
Comet form of a Starfish, showing how one arm "regenerates" or reproduces other four.—From Carus Sterne, after Haeckel.

kous region is set free, breaks up into fragments, liberates the germ-cells, and dies. All the swarming portions which make the water for a short

time "like vermicelli soup" are headless. The intact worm seems to live in the crevices of the coral reef.

(*c*) In Syllideæ the epitokous segments separate and bud out a head; the atokous segments also survive, and have the power of forming new segments.

Starfishes and the like surrender their "arms" so readily, that some have supposed that they might, in this way, normally multiply. A voluntary surrender of parts as a mode of multiplication is, however, in this case difficult to prove. It is said to occur in *Cucumaria planci*, one of the sea-cucumbers. While crustaceans, insects, spiders, and molluscs may lose and regrow certain parts, no asexual multiplication occurs.



Adventitious buds forming at the sides of a leaf of *Bryophyllum calycinum*.—From nature.

In the tunicates the asexual process has again full play. It is not confined to the passive sessile forms, where one might expect it, but occurs in some of the free-swimmers as well. From a creeping stem buds may arise, like plants from a rhizome; or a parent form may bud off all round, and finally die away, leaving the offspring in a circle round a cavity. Both by budding and division chains may be formed, as in the salpas. In these lowly vertebrates asexual multiplication terminates. How the process often alternates in regular rhythm with ordinary sexual reproduction will be discussed in the next chapter.

SUMMARY.

1. Artificial division may be readily utilised as a means of multiplication in plants and in lower animals.

2. Regeneration of lost parts is very common both in plants and animals.

3. Asexual reproduction from continuous budding to discontinuous multiplication has many degrees.

4. It occurs in many types from Protozoa to Tunicata.

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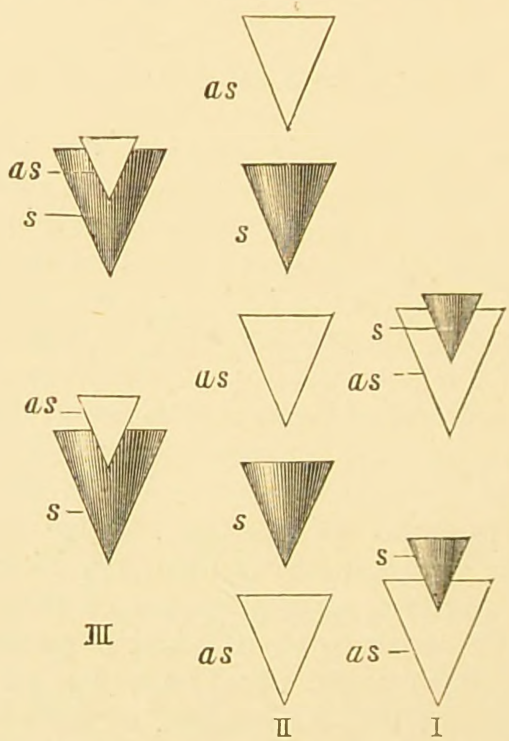
CHAPTER XV.

Alternation of Generations.

§ 1. *History of Discovery.*—Early in the century the poet Chamisso, accompanying Kotzebue on his circumnavigation of the globe, observed in one of the locomotor tunicates (*Salpa*) that a solitary form gave birth to embryos of a different character, connected together in chains, and that each link of the chain again produced a solitary form. Chamisso's observation does not seem to have been quite accurate, but there is no doubt that he first called attention to what is by no means an uncommon fact, that an organism produces an offspring very unlike itself, which by and by gives origin to a form like the parent. The progress of marine zoology and the study of parasitic worms gave naturalists like Sars, Dalyell, Lovén, Von Siebold, and Leuckart, early glimpses of many alternations in life-history, but Steenstrup was the first to generalise the results. This he did (1842) some twenty years after Chamisso, in a work entitled "On the Alternation of Generations; or, The Propagation and Development of Animals through Alternate Generations, a peculiar form of fostering the young in the lower classes of animals." From hydroids and flukes, he gave illustrations of the "natural phenomena of an animal producing an offspring, which at no time resembles its parent, but which itself brings forth a progeny that returns in its form and nature to the parent." The interpolated generation he distinguished by the name of "Amme" or "wet-nurse." In 1849, Owen submitted Steenstrup's essay to stern criticism, rejecting especially the metaphorical name "nurse" as but a verbal explanation, and proposing to explain what he also called "alternation of generations," along with parthenogenesis and other phenomena, by the supposition of a residual germ force or spermatic power in the cells of the apparently asexual offspring. In this he partially prophesied the modern conception of a residual persistent germ-plasma. Soon afterwards Leuckart

attempted to treat all as cases of metamorphosis, thereby greatly extending the meaning of that term. The labours of some of the foremost naturalists have both extended Steenstrup's observations and rendered them more precise. We now know that the phenomenon is of wider occurrence than was at first supposed, and also that the title has been unduly extended to cover



Diagrammatic representation of alternation of generations, *as*, asexual generation; *s*, sexual generation.

II. Shows alternation of asexual (*as*) and sexual (*s*) generations.

In I. the sexual is becoming increasingly subordinated to the asexual (as in flowering plants).

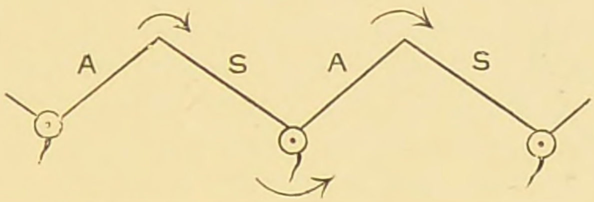
In III. the asexual is increasingly subordinated to the sexual (in mosses).

several entirely different sets of facts. It is necessary, therefore, to notice the various forms which the rhythm of reproduction may take.

§ 2. *The Rhythm between Sexual and Asexual Reproduction.*—The clearest case to start with is that of many hydroids. A sessile, plant-like zoophyte, which buds off numerous nutritive persons, produces in the warm months modified individuals which are set adrift as medusoid persons. Unlike the hydroid which bore them, these become sexual; and from their fertilised

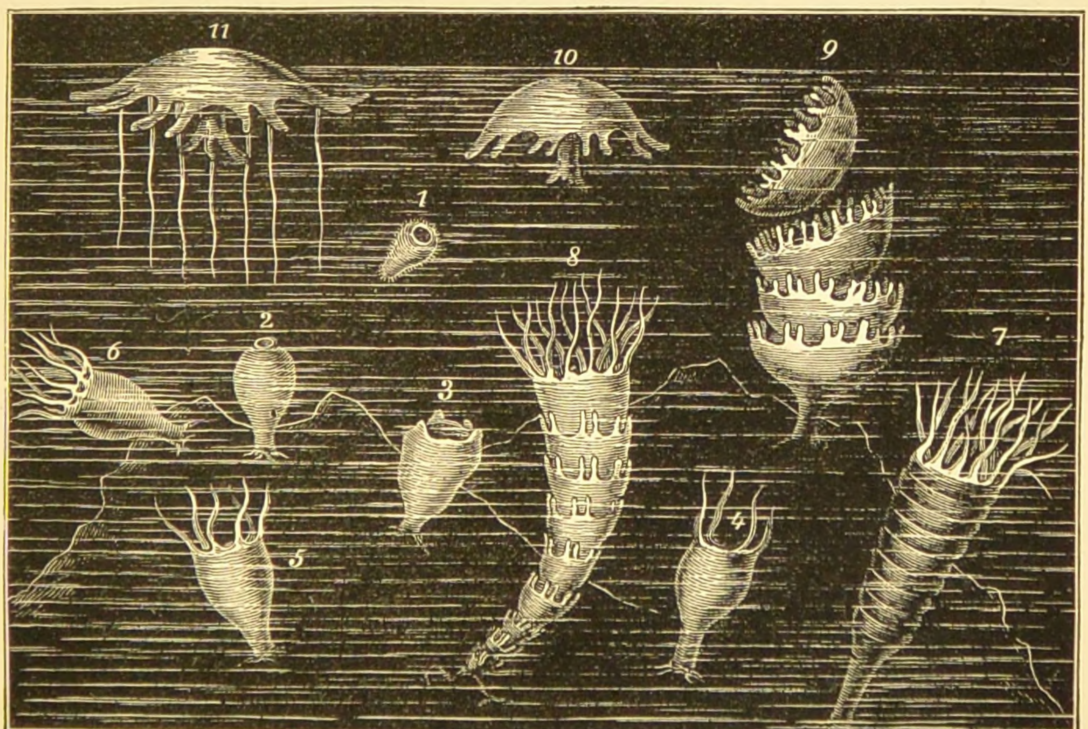
ova an embryo develops, which eventually settles down to start a new sessile colony. And thus through the seasons we have hydroid asexually producing sexual medusoids, and these again producing hydroids. The life-history for two complete rhythms may be written in the formula, in which M, F, and A stand for male, female, and asexual forms respectively,—

$$\frac{M}{F} - A - \frac{M}{F} - A - \frac{M}{F}$$



A, asexual hydroid ; S, sexual medusoid ; fertilised ova at base.

Or take, in slight contrast, the life-story of the common jelly-fish Aurelia. Large free-swimming sexual animals produce ova which are fertilised by sperms ; the embryo develops, not how-



The alternation of generations in the common jelly-fish *Aurelia* ; 1, the free-swimming embryo, or planula ; 2, the embryo settled down ; 3, 4, 5, 6, the developing asexual stage, or hydra-tuba ; 7, 8, the formation of a pile of individuals ; 9, the liberation of these ; 10, 11, the acquisition of the free-living sexual medusa form.—From Hæckel.

ever into a jelly-fish, but into a sessile hydroid-like organism or "hydra-tuba." By growth and division this asexually produces the jelly-fish in turn. Here the sexual generation is more stable and conspicuous, the reverse of the former case, but the same formula applies.

Or take a case from another class of animals, the marine worms. Some of the syllids have the following life-history. A worm remains asexual, never attaining either the external characteristics or the internal organs of the sexual individuals. It gives rise to these, however, by an asexual process of chain-making. Sexual individuals are budded off from the asexual, into which their fertilised ova in turn develop. This must, of course, be distinguished from cases where asexual multiplication is only a phase preceding the acquisition of sexuality The above cases are again expressible in the simplest formula.

Now take a more complex case, from among the tunicates, the highest point at which the genuine alternation can be said to occur. From the single ovum of a sexual Salpa an asexual individual develops which remains for a time connected with its parent. It eventually escapes and becomes free-swimming, and after a time forms a process or stolon on the surface of which buds are formed. The buds develop and form a chain of individuals. Then the stolon with its chain is set free from the asexual parent, and the links of the chain become sexual Salpæ.

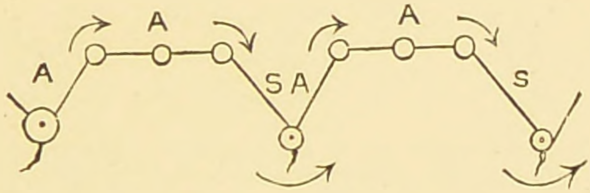
In the allied *Doliolum* the life-history is more complicated. A sexual form gives rise sexually to tailed asexual larvæ; the larva loses its tail and forms two processes or dorsal and ventral stolons; buds from the ventral stolon migrate to the dorsal stolon and develop there into a second set of asexual forms; the dorsal stolon also forms buds on its own account; some of these individuals on the dorsal stolon are set adrift, and each develops a ventral stolon from which the young sexual forms arise. There are thus several asexual generations between one sexual stage and the next.

§ 3. *Alternation between Sexual and Degenerate Sexual Reproduction.*—The cases we have just noticed are both easier to state and easier to explain than others which are sometimes also included under the vague title of "alternation of generations." The above alternations were between sexual and asexual reproduction, and must be distinguished, vague as the boundary must be, from alternation between the ordinary sexual process and a degenerate form of the same.

The history of some of the flukes (Trematoda) may be taken as a first

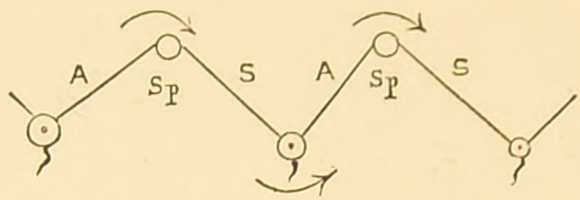
illustration. The common liver-fluke (*Distomum* or *Fasciola hepatica*) which causes the disastrous "rot" in sheep has a life of vicissitudes. The fertilised ovum gives rise to an embryo; this passes from the sheep, which its sexual parent infested, to the water by the field side. There it leads for a few hours an active life, knocking against many things, but finally attaching itself to a minute water-snail (*Limnæus truncatulus*). Into this it bores, losing its covering of active cilia with change of habit, and becoming much altered into a passive vegetative form known as a sporocyst. Now this sporocyst sometimes divides; and if this were all, and the results grew up into liver-flukes, we should have the old formula and less loss of sheep. But direct development never occurs, and we may leave the casual division at present out of account. Certain cells within the sporocyst develop like parthenogenetic ova. They produce within the body of the sporocyst another brood of what are called *Rediæ*. There may be several generations of rediæ, but the final result is a brood of minute tailed organisms (*Cercariæ*), which leave the water-snails, leave the water even, creep up grass stems, and encyst themselves. There most wait for death, a few for the attainment of adult sexual life if they chance to be eaten by a sheep.

This cannot be accurately ranked as parallel to what occurs among the above-mentioned tunicates, for the rediæ arise from precocious reproductive cells. These cannot be called ova, and there is no fertilisation, but yet the process is not one of division, or of budding. It is a degenerate process of parthenogenetic reproduction in early life. The facts may be again summed up in a formula, which does not take account of the occasional division of the "sporocyst."



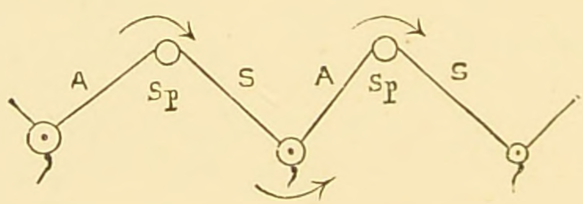
A, asexual larvæ; S, sexual fluke; the upper circles represent the special reproductive cells; fertilised ova at the base.

This alternation between sexual reproduction with the usual fertilisation, and reproduction by means of special cells which yet require no fertilisation, prevails in many plants, *e.g.*, ferns and mosses. From a fertilised egg-cell the ordinary fern-plant, with which every one is familiar, develops. But this is quite asexual, if we mean by that that it is neither male nor female, and that it produces neither male nor female elements At the same time it produces special reproductive cells,—not egg-cells exactly, any more than those within the sporocyst were, but yet able to develop of themselves into a new organism. This is not another fern-plant, however, but an inconspicuous green organism, much less vegetative, and sexual. The so-called "spore" formed on the leaves of the sexless fern-plant falls to the ground, develops a "prothallus," which bears male or female organs, or both. An egg-cell is fertilised by a male element, and the conspicuous vegetative fern-plant once more arises. The formula is therefore as follows:—



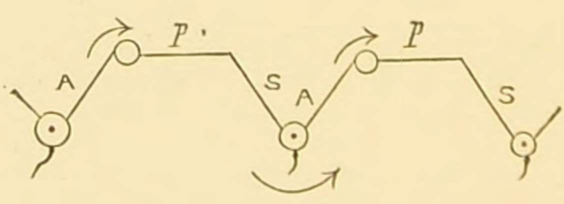
Where A = sexless vegetative fern-plant;
sp. = the parthenogenetic special reproductive cell or spore;
S = the sexual inconspicuous "prothallus," with male and female organs.

Now take the history of a moss. Unlike the fern, the more conspicuous "moss-plant" is sexual. It bears male and female organs, and an egg-cell is fertilised by a male element. The fertilised egg-cell, however, does not lose its hold of the mother plant, but grows like an encumbering parasite upon it. Obviously, then, it does not give rise to another "moss-plant." The result of the fertilised egg-cell is a tiny sexless stalk, which bears on its apex the special reproductive cells or spores with which we are now familiar. In other words, the fertilised egg-cell develops into a parasitic spore-bearing generation. The "spores" fall into the ground, as they did in the fern, and there grow into a usually thread-like structure, from which the sexual moss-plants are budded off. If we do not emphasise the transitional thread-like stage,—the protonema as it is called,—the formula is as follows:—



Where A = inconspicuous sexless parasitic generation upon the "moss-plant";
sp. = the special parthenogenetic reproductive cell or spore produced by A;
S = the conspicuous sexual "moss-plant," budded from the threads developed from the spore.

If we do emphasise the "protonema" stage (*p*), and regard the moss-plants as asexually budded from it, the formula runs:—

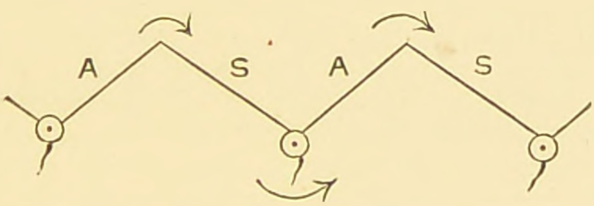


In the fern, the vegetative sexless generation was the more conspicuous; in mosses, the sexual generation. In a way this recalls the contrast between the life-history of many a zoophyte, and that of the common jelly-fish *Aurelia*. The asexual hydroid colony is more conspicuous than

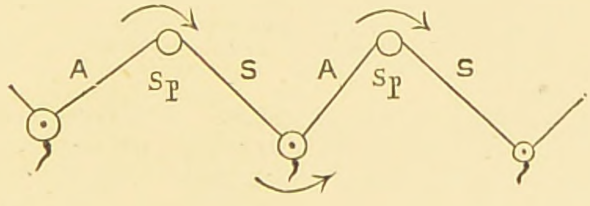
the usually small swimming-bell, but the sexual jelly-fish is much more conspicuous than the minute asexual "hydra-tuba." The common comparison between medusoid and hydroid on the one hand, and prothallus and fern-plant on the other, is rather misleading, simply because the hydroid merely buds off the medusoid, while the fern-plant produces the prothallus from a special reproductive cell or spore. In some ferns and mosses, however, a more exact parallel is occasionally exhibited. The production of "spores" may be suppressed, and from the place where they should be formed a (sexual) fern-prothallus or a new (sexual) moss-plant is vegetatively developed, just as medusoid from hydroid. This exceptional occurrence is technically called *apospory*. The very opposite of this also occurs, the suppression not of the spore-bearing, but of the sexual generations. The fern-plant then arises vegetatively from the prothallus; and this would be paralleled if we supposed the sporocyst of the fluke to bud off rediæ (as it sometimes does), and these to continue the species without ever becoming really sexual, solely by means of the special cells above described. This is called *apogamy*.

Apogamy has also been described by Treub in the remarkable flowering plant *Balanophora*, where the abortion and disappearance of the egg-apparatus is closely parallel to what occurs in one of the brackens (*Pteris cretica*). ("Ann. Jard. Bot. Buitenzorg," xv., 1898, pp. 1-25, 8 plates.)

§ 4. *Combination of both these Alternations.*—The asexual hydroid buds off a medusoid, the fertilised ovum of which develops into a hydroid. Here there is simple alternation between sexual and asexual reproduction.

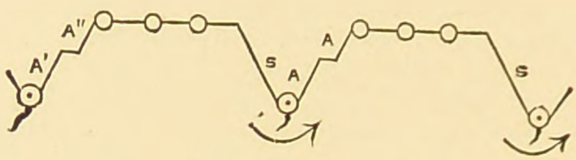


A sexless fern-plant forms special reproductive cells (spores), which develop parthenogenetically into a sexual prothallus, from the fertilised egg-cell of which the fern-plant arises.



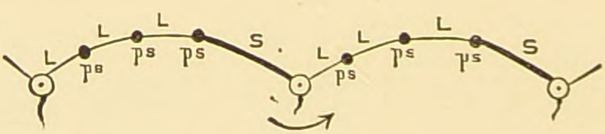
The difference between these two alternations has been as often pointed out as it has been ignored. The former is called true alternation of generations (or metagenesis); the latter is called by zoologists, in reference to flukes for instance, *heterogamy*. Comparisons between the alternations in plants and animals have seldom recognised the distinction.

Let it be recognised, however, and we can readily proceed to more complicated cases where the two are combined. Returning to the liver-fluke and others like it, we find that the sporocyst sometimes multiplies in a genuinely asexual fashion—without the intervention of precocious ova, special reproductive cells, germs, or spores, as they may be called—by direct division or budding. For such cases the formula must be modified as follows:—



The complication is not serious. It is simply that, before the multiplication by special cells sets in, there may be more than one (A′, A″) entirely asexual (and not merely sexless) generation.

§ 5. *Alternation of Juvenile Parthenogenetic Reproduction with the Adult Sexual Process.*—We have already noted the curious precocity of some midge larvæ, which reproduce while still young. Cells within the body, apparently precocious ova, develop parthenogenetically into larvæ, which prey upon the mother larva, eventually kill her and leave her, only themselves to become in turn similar victims of precocity. This may continue for a series of generations, with continuous decrease in the size of the reproductive cells, till finally true sexuality and adult life is attained. The reproductive cells here are rather more differentiated than those in the young flukes, but the close parallelism is indubitable. Except that there is for a while no fertilisation, the process can hardly be called asexual. The formula may be expressed in a gentle curve:—

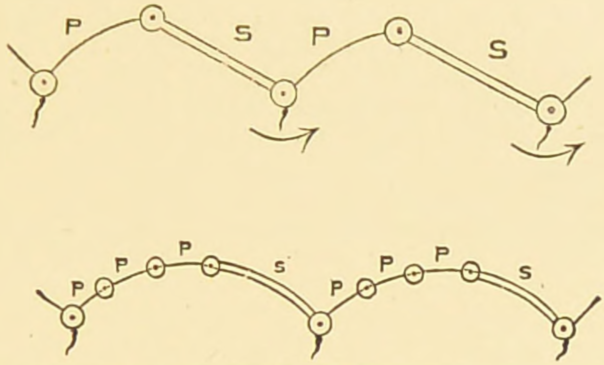


Where the starting-point is as before a fertilised ovum;
L = prematurely reproductive larva;
ps = precocious parthenogenetic "pseudova";
S = adult sexual male or female organism.

Somewhat different is the curious case of *Gyrodactylus*, a trematode parasitic on fresh-water fishes, where three generations are found enclosed, one within the other, in a fashion which recalls the fancies of the preformationists. In this case, however, it seems likely that internal fertilisation really occurs.

§ 6. *Alternation of Parthenogenesis and Ordinary Sexual Reproduction.*—In our gradual ascent, we now reach the frequent alternation of parthenogenesis and ordinary sexual reproduction. The special cells which develop without fertilisation are now genuine parthenogenetic ova, and the organisms which produce them are adults, not juveniles. The formulæ will

differ mainly in the number of generations through which the parthenogenesis may be continued.



Where the starting-point is a fertilised ovum ;
P = parthenogenetic female, producing a parthenogenetic ovum, from which arise other parthenogenetic forms, or eventually ;
S = male and female.

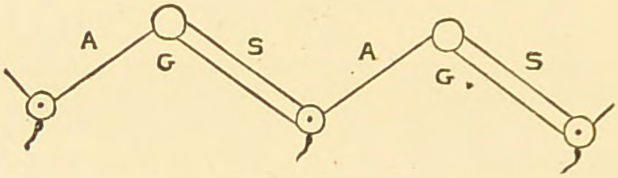
§ 7. *Alternation of Different Sexual Generations.*—The rhythm may be followed in yet a higher scale. In a very few cases there is an alternation between two different *sexual* generations. Thus one of the threadworms (*Leptodera appendiculata*) found in the snail gives rise, by the ordinary sexual process, to a different form, which leads a free life, and subsequently gives origin to the parasite. In both generations the sexes are distinct. More remarkable still is the history of another nematode (*Angiostomum nigrovenosum*), found in the lung of the frog. It is physiologically hermaphrodite, though its organ is ovary-like; its eggs are fertilised by its own sperms, which mature first; the progeny become sexual —males and females—in the earth, and their offspring return to the frog, where they become hermaphrodites. Another example of alternation of sexual generations is found in one of the threadworms which occur in man (*Rhabdonema strongyloides*).

§ 8. *Occurrence of these Alternations in Animals.*—From sponges to tunicates such alternations occur. Beyond the latter, unless we wish to be very subtle, they cease. It is necessary to be clear about the fact that asexual and sexual reproduction may occur together in the same form. The common hydra gives off buds in an entirely asexual way, but it is also a sexual animal, with male and female organs. There may be periods of vegetative growth and climacterics of sexuality in the same organism, without any alternation of generations

It is possible that the term alternation of generations may be applied to some of the phenomena observed in the Protozoa. Thus Brandt maintained that all the colonial radiolarians, known as Sphærozoa, form on the one hand *isospores*, which are all equal and apparently parthenogenetic, and on the other hand *anisospores*, which are large and small,—in fact, sexually dimorphic. He believes—though the fact cannot be called demonstrated—that two unequal anisospores unite to form a double cell, a fertilised unit, which will produce isospores again, and these the normal colony. The generation of these Sphærozoa is further complicated (*a*) by division of the colonies, (*b*) by division of the individuals of young vegetative

colonies, and (*c*) by the formation of special "extra-capsular" reproductive bodies in young colonies.

The history of the common fresh-water sponge (*Spongilla*), as told by Marshall, is one of many vicissitudes. In autumn the sponge begins to suffer from the cold and scarcity of food. It dies away; but some of the units save themselves, and, in a sense, the parent, by forming the "gemmules" we have already noticed. These winter in a quiescent state within the parental corpse, but in spring they get out of the debris, and start male or female sponges. The males are short-lived, but their male elements fertilise the ova of the females. The fertilised ovum develops into a ciliated embryo, and this into an asexual sponge, which produces the gemmules.



The starting-point a fertilised ovum, which develops into
A = asexual sponge, which forms only
G = gemmules, which develop into
S = male and female sponges.

Besides the hydroid and medusoid, the hydra-tuba and jelly-fish alternations, which we have already noticed, there are many complications of degree among cœlenterates. The medusoid stage degenerates by subtle gradations, ceasing to be free, and eventually becoming what, if its history were not known, would be called an organ rather than a "person" of the colony. Furthermore, it may itself take to budding, and continue the asexual habit of the hydroid from which it springs. Outside the Hydrozoa, genuine alternation of generations does not occur, unless that described by Semper for Fungia corals be accepted as such.

A very interesting alternation has been described by W. K. Brooks in a remarkable medusa (*Epenthesis macradyi*). On the reproductive organs of this swim-bell there grow, like parasites, what are exactly comparable to the reproductive buds (blastostyles) of a hydroid, and these form medusoids by budding. The result is a compound colony, which approaches the Siphonophora. The process recalls and surpasses the apogamy of a few ferns.

Among worm-types, the strict alternation of generations in some of the marine chætopods (syllids), the more complicated phenomena of so many trematodes, the sexual rhythms of that peculiar threadworm *Angiostomum*, have been already discussed. It is necessary, however, to state the case for tapeworms, which are usually included among the examples of alternation of generations. The usual view is, that the embryo of a tapeworm develops into an asexual bladder-worm, which asexually buds off a "head," or more than one. Such a "head," passing to another host, buds off asexually the chain of reproductive joints or sexual individuals which constitute a tapeworm. Asexual bladder-worm, asexual "head," and sexual joints, form the series. That there is a genuine alternation of generation is believed by some authorities, but there are emphatic difficulties against this supposition, except in the occasional occurrence of a bladder-worm with several "heads," each of which may develop into a tapeworm. The

case is well stated by Hatchett Jackson in his monumental edition of Rolleston's "Forms of Animal Life," and we accept his verdict that there is really one individual throughout, except when asexual multiplication of heads occurs. The tapeworm, on this view, is an adult sexual bladder-worm, and the joints are only highly individualised segments.

Of the parthenogenetic cycles in crustaceans and insects, the juvenile reproduction of some of the latter, and the true alternation of generations in some tunicates, enough has already been said.

Von Jhering is responsible for starting the paradox that in higher animals a mother may bring forth her grandchildren. He refers to the case of the hyæna-like edentate *Praopus*, where a single ovum gives rise to eight embryos, which are thus in a pedantic sense grandchildren! The frequent occurrence of twins in all groups, the remarkable case of an earthworm (*Lumbricus trapezoides*) in which a double embryo is constant, and the morphological resemblance of polar globules to abortive germs, led Von Jhering to maintain that the origin of multiple embryos from a single ovum is the primitive and normal condition, and that the development of only one is secondary and adaptive. The data are hardly sufficient for such a striking conclusion.

Paul Marchal has described in regard to *Encyrtus fuscicollis*, one of the parasitic Hymenoptera, which lays its eggs in those of another insect, *Hyponomeutes*, the remarkable peculiarity that the ovum gives rise not to one embryo, but to "a legion of small morulæ," forming a chain of 50-100 embryos. The amniotic envelope loses its vesicular form and becomes a long flexible tube, within which lie the embryos surrounded by granular material apparently derived from a disruption of part of the original egg. As the author says, this is a mode of reproduction unique among Arthropods, if not among animals. ("Comptes Rendus," cxxvi., 1898, pp. 662-4.)

§ 9. *Beard's Hypothesis of Alternation in Vertebrates.*—Beard has propounded a somewhat subtle theory which suggests that there is a disguised alternation of generations in vertebrate animals, just as there is in flowering plants. In several invertebrate types, *e.g.* Echinoderms and *Phoronis*, the egg gives rise to a larva which does not directly develop into the definitive organism, but serves as the foundation on which the development recommences as it were *de novo*. Similarly, Beard believes that in Vertebrates, whether skate or chick, there are traces of an asexual larval stage on the top of which the embryo proper develops. At the "critical stage," when the embryo begins to put on its generic and specific characters, it also sets about the task of suppressing the larval foundation. ("On Certain Problems of Vertebrate Embryology," Jena, 1896, vi. and 77 pp.)

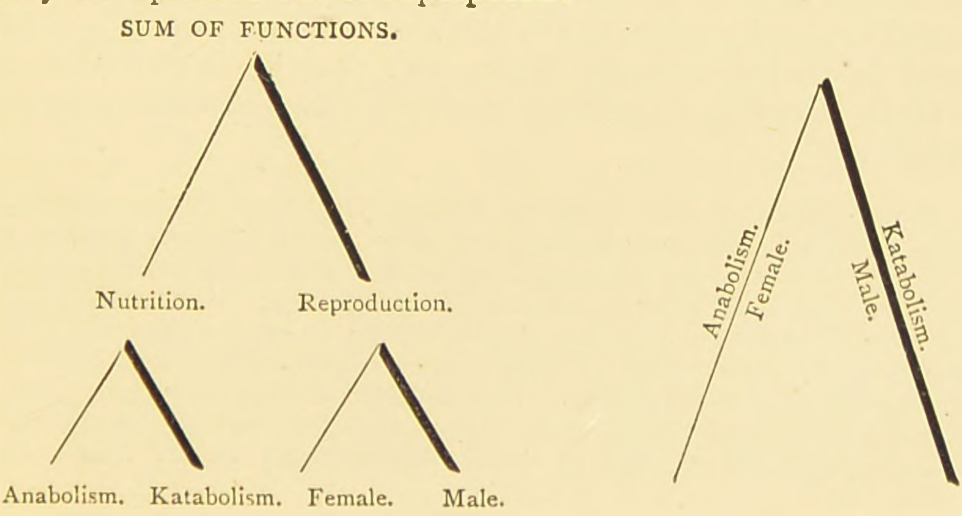
§ 10. *Occurrence of Alternations in Plants.*—In the lower plants, algæ and fungi, an alternation between spore-producing and truly sexual generations is frequent. In mosses and ferns it is almost constant, and yet more marked. Occasionally either spore-formation or sex-cell formation may be suppressed, and the life-history thus simplified. In a few of the higher plants both are exceptionally suppressed, and we have thus a reversion to a purely vegetative process, just as if a hydra went on giving off daughter-buds without ever becoming sexual. In the

flowering plants, what corresponds to the sexual generation of a fern is much reduced; it has come to remain continuous with the vegetative asexual generation, on which it has reacted in subtle physiological influence. Just as in the higher animals, alternation of generations finds at most only a rudimentary expression.

§ 11. *Heredity in Alternating Generations.*—The problem of the relative constancy of inheritance is now in part solved by the theory of germinal continuity. The ovum which develops into an offspring is virtually continuous with the ovum which gave rise to the parent. A chain of ovum-like *cells* is only demonstrable in a few cases; but Weismann overcomes this difficulty, by supposing that what really keeps up the protoplasmic tradition or continuity between the parental ovum and the next generation, is a specific and stable portion of the nucleus,—the "germ plasm." When a medusoid goes off from a hydroid, it carries with it a legacy of this germ-plasm, continuous with that which gave rise to the hydroid. This legacy forms the reproductive elements of the medusoid, which in turn give rise to hydroids. The medusoid itself is a modified asexual growth, into which some of the germ-plasm of the hydroid has migrated; it is literally only the bearer or trustee of the hydroid germ-plasm. Weismann's classic researches on hydroids have shown that the reproductive cells, which, by hypothesis, bear the germ-plasm, often arise far down in the hydroid body, and actually migrate to their final seat in the bearer. Where the alternation is not between sexual and asexual, but between the ordinary sexual process and multiplication by special parthenogenetic cells, as is the case in many flukes, we may in the same way suppose that the cells within a sporocyst which give rise to rediæ are, like ova, charged with this reproductive germ-plasm. It is very interesting to notice that, as far back as 1849, Owen had a distinct prevision, not only of the distinction between body-forming cells and reproductive-cells, of which so much is now made, but of the essential idea of the "germ-plasm." Speaking of the recurrence of a parental form after numerous interpolated generations, he says, "the essential condition is the retention of certain of the progeny of the primary impregnated germ-cell, or, in other words, of the germ-mass unchanged in the body of the first individual developed from that germ-mass, with so much of the spermatic force inherited by the retained germ-cells from

the parent-cell or germ-vesicle as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them." In this somewhat over-weighted sentence, if we read "germ-plasm" instead of "spermatic force," we have a close approximation to the modern conception of Weismann. Again, Owen says, "an impregnated germ-cell imparts its spermatic power to its cell-offspring; but when these perish, or when the power is exhausted by a long descent, it must be renewed by fresh impregnation. But nature is economical, and so long as sufficient power is retained by the progeny of the primary impregnated vesicle (the essential part of an ovum), individuals are developed from that progeny without the recurrence of the impregnating act."

§ 12. *Hints as to the Rationale of Alternation.*—The puzzle of alternation may be lessened if we consider the physiological aspect of the facts. A fixed hydroid contrasted with a swimming-bell or medusoid, a sessile hydra-tuba contrasted with an actively locomotor jelly-fish, illustrate not a peculiar antithesis, but a most general and fundamental rhythm of organic life,—that between nutrition and reproduction. The hydroid has a relatively passive habit and a copious nutrition; it is preponderatingly vegetative and asexual. The reverse habit, the physiological rebound, finds expression in the medusoid. In the same way, though the alternation is less strictly between asexual and sexual, the contrast between leafy spore-bearing fern-plant and inconspicuous sexual prothallus is again fundamentally parallel. The notation adopted must have already suggested our fundamental diagram, the different forms of which may be separated out or superposed:—



Although it has just been shown that the process of alternation demands a much more thorough analysis and discrimination of the different cases than has hitherto been customary, and this on the physiological as well as merely on the morphological side, the general aspect of the process, in which an asexual form alternates with one or more dimorphic sexual generations, makes it evident that we have here to do in two generations with what is often so obvious in one,—the familiar antithesis between nutrition and reproduction. A consideration of the physiological distinctions between the asexual and sexual generations, shows that the former is the expression of favourable nutritive conditions resulting in vegetative growth, or at most in asexual multiplication, while the latter is conditioned by less propitious circumstances. Just as a well-nourished plant may continue propagating itself by shoots and runners, and just as an aphis in artificial summer may for years reproduce parthenogenetically, so a hydroid with abundant food and otherwise favourable environment may be retained for a prolonged period vegetative and asexual, while dearth of food and otherwise altered conditions evoke the appearance of the sexual generation. The contrast between the deeply-rooted well-expanded fern-plant and the weakly-rooted slightly-exposed prothallus, is obviously that between an organism in conditions favourable to the continuance and preponderance of anabolic processes, and an organism in an environment where katabolism is, at an early stage, likely to gain relative ascendency. The former is thus naturally asexual, the latter sexual. A survey, in fact, of the conditions and characteristics of the two sets of forms, inevitably leads us to regard the asexual generation as the expression of relatively predominant anabolism, and the sexual as equally emphatically katabolic. Alternation of generations in its less complex forms may thus be described as a rhythm between a relatively anabolic and katabolic preponderance.

§ 13. *Origin of Alternation of Generations.*—Even in an individual plant or animal there are vegetative and reproductive periods; alternation of generations involves the separation of these to different individuals, by the interpolation of more or less asexual reproduction. In most hydroids, the asexual vegetative tendency preponderates; in most medusoids, great activity is dominant. But the origin in each particular case is involved in the pedigree of the organism. Thus Haeckel distinguishes a progressive from a retrogressive origin; in the former, the organisms are in transition from preponderant asexual to sexual reproduction; in the latter, the

organisms are returning or degenerating from dominant sexuality to an asexual process. It is safe to say that the latter is more frequently the right interpretation of the facts. So far as reproduction is concerned, one of those medusoids (Trachymedusæ) which have no corresponding hydroid parent, or a jelly-fish like *Pelagia* which has no fixed asexual hydra-tuba stage, is nearer the ancestral habit than those members of both divisions which exhibit alternation of generations. In regard to alternating series of similar forms with different degrees of sexuality, *e.g.*, parthenogenesis and true sexual reproduction in aphides, Weismann suggested that the alternation may be associated with the periodic action of external influences ("Studies in the Theory of Descent," chap. v.). But in contrast to such cases he distinguished, (*a*) an origin from metamorphosis, where one stage in the life-history becomes precociously reproductive, *e.g.*, in the midge *Cecidomyia;* (*b*) the case of the Hydromedusæ, where sexuality is postponed in early life, and asexual reproduction dominates; and (*c*) an origin from division of labour within a colony. Without entering upon a discussion of each case in relation to its history and environment, it is not possible to do more than reassert that in many different degrees the continuous alternation between growth and multiplication, nutrition and reproduction, asexuality and sexuality, anabolism and katabolism, may express itself in the life-history of the organism.

SUMMARY.

1. The fact that successive generations may be markedly different was observed by the poet Chamisso, and first made precise by the zoologist Steenstrup.

2. A fixed asexual hydroid buds off and liberates locomotor sexual medusoids, whose fertilised ova give rise again to hydroids. Asexual and sexual generations alternate.

3. The offspring of the liver-fluke forms from certain cells in its body a numerous progeny; these repeat the same process several times; the last generation grow into the sexual liver-flukes. Reproduction by special cells, like precocious undifferentiated ova, alternates with reproduction by ordinary fertilised ova. So too the vegetative sexless "fern-plant" gives rise to spores, which develop into an inconspicuous sexual prothallus. From the fertilised egg-cell of the latter the "fern-plant" arises.

4. These two different kinds of alternations (§ 2 and § 3) may be combined in a more complicated manner.

5. In some flies precocious parthenogenetic reproduction alternates with the normal sexual reproduction of the adults.

6. In many insects and crustaceans, parthenogenetic reproduction alternates with the normal sexual process. There may be one or many intervening parthenogenetic generations.

7. A hermaphrodite threadworm parasitic in the frog fertilises its own eggs, which develop into free-living males and females, from the fertilised ova of which the hermaphrodite parasites again arise. Here there is an alternation of sexual generations.

8. The occurrence of these various alternations is widespread, from sponges to tunicates.

9. Beard's hypothesis of alternation in vertebrates.

10. In plants they occur in algæ and fungi, are almost constant in ferns and mosses, but are inconspicuous in higher plants.

11. The problem of heredity is somewhat complicated by such alternations.

12. Alternation of generations may be described as a rhythm between a relatively anabolic and katabolic preponderance.

13. Alternation of generations has probably arisen in various quite distinct ways.

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BOOK IV.

THEORY OF REPRODUCTION.

CHAPTER XVI.

Growth and Reproduction.

§ 1. *Facts of Growth.*—In a well-known aphorism Linnæus noted that living organisms are not alone in their power of growth. Crystals become centres for other crystals, till a large mass results; and the product, as every case of minerals shows, is often both orderly and complex. But there are great differences between organic and inorganic growth, one of the most obvious being that the organism is able to grow larger at the expense of material different from itself, while the crystal can only increase out of material similar to itself. The grass grows at the expense of water, soil, and air; and the foal grows at the expense of the grass, but a dead thing cannot grow in this way. Probably of much less importance is the old distinction that the growth of organisms has a peculiar method of its own, that of intussusception as distinguished from mere accretion. The new particles which are taken in, more than replacing previous expenditure, are not deposited upon the surface of already established material, as is the case with a crystal, but are intercalated in the interstices of previous particles. We cannot enter here upon the long-continued controversy, whether such structures as the cell-wall and starch-grains of plants grow thicker or larger by accretion in crystal-like fashion, or by intercalation which is supposed to be characteristically organic. It is worth noticing, however, as Bütschli points out, that if the living matter has the form of an intricate network, the fresh material of replacement or growth may be added to the surfaces of the threads which make the web. Thus what is roughly called intercalation may be more literally an internal accretion.

Hunger is a dominant characteristic of living matter. When a unit mass or cell has been giving off energy in doing any kind of work, its substance is chemically impaired,—less capable of doing further work until new energy has been supplied by

nutrition. The supply which the lifelong hunger of the protoplasm demands, is frequently afforded in greater abundance than the actual necessities require. There is a surplus for further upbuilding after mere reparation has been made. This surplus is the condition of growth. In other words, growth or addition to the capital of the organism occurs when income is in excess of expenditure, when construction preponderates over disruption.

But beside this familiar fact, it is necessary to place another certainty, that of the limit of growth. There are among the Protozoa a few giants, such as the large amœboid *Pelomyxa*, some of the gregarines, and even more markedly the extinct nummulites, which were sometimes as large as half-crowns. So an occasional alga, like *Botrydium*, may swell out into a large single cell, and the ova of animals, *e.g.* birds, are often greatly expanded by the accumulation of yolk. Yet cells generally remain very small. They have their maximum size, approximately constant for each species. Up to this point they grow, but no further. The same, as every one knows, is true of most multicellular animals. The size fluctuates slightly according to the conditions of individual life, but the average is strikingly constant.

§ 2. *Spencer's Theory of Growth.*—The first adequate discussion of growth is due to Spencer. He pointed out, that in the growth of similarly shaped bodies the increase of volume continually tends to outrun that of the surface. The mass of living matter must grow more rapidly than the surface through which it is kept alive. In spherical and all other regular units the mass increases as the cube of the diameter, the surface only as the square. Thus the cell, as it grows, must get into physiological difficulties, for the nutritive necessities of the increasing mass are ever less adequately supplied by the less rapidly increasing absorbent surface. The early excess of repair over waste secures the growth of the cell. Then a nemesis of growing wealth begins. The increase of surface is necessarily disproportionate to that of contents, and so there is less opportunity for nutrition, respiration, and excretion. Waste thus gains upon, overtakes, balances, and threatens to exceed repair. Suppose a cell to have become as big as it can well be, a number of alternatives are possible. Growth may cease, and a balance be struck; or the form of the unit may be altered, and surface gained by flattening out, or very frequently by

outflowing processes. On the other hand, waste may continue on the increase, and bring about dissolution or death; while closely akin to this, there is the most frequent alternative, that the cell divide, halve its mass, gain new surface, and restore the balance. Independent suggestions, similar to Spencer's, have been made by Professor Leuckart and Dr. Alexander James.

§ 3. *Cell-Division.*—What usually occurs, then, at the maximum or limit of growth, is that the cell divides. This, in its simplest forms, is rough enough to suggest rupture or overflow;

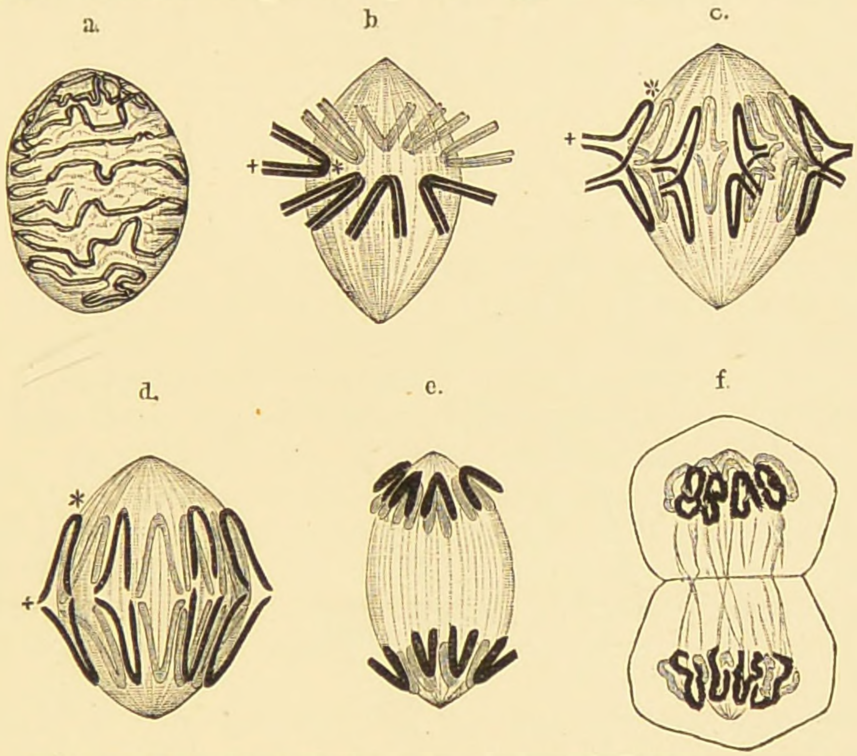
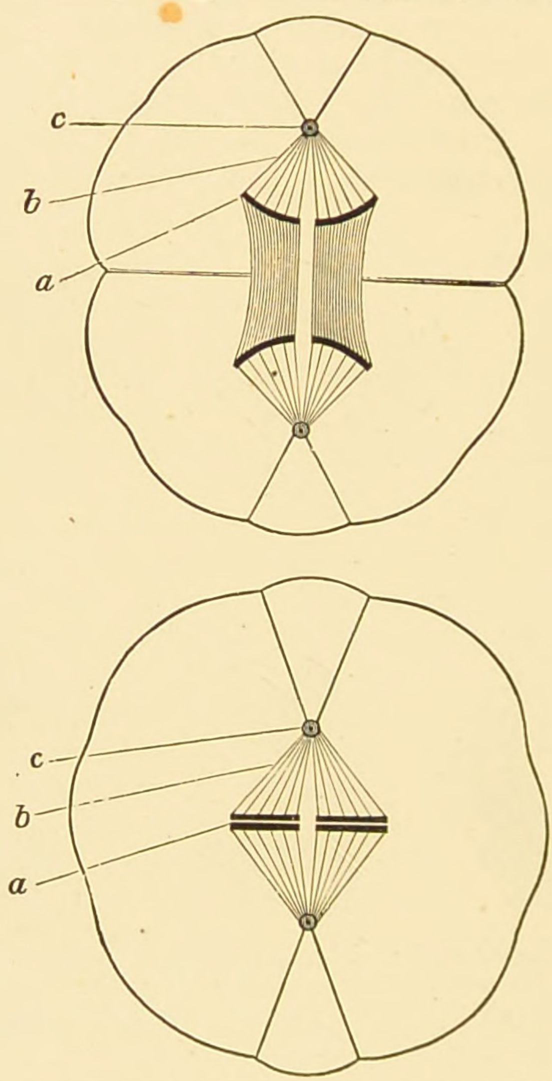


Diagram of the changes in the nucleus during cell-division:—coil stage (*a*), the formation of a double star (*b*, *c*, *d*), and the recession of the divided chromatin elements to opposite poles (*e*) to form the daughter-nuclei (*f*) of the two daughter-cells. The centrosomes are not shown.—From Hatschek, after Flemming.

but in the vast majority of cases it is an orderly and definite process, in which the nucleus plays an important part, and the centrosomes behave as if they were intimately concerned with the mechanism of division. By a complicated series of changes, both in form and position, the essential nuclear elements group themselves so as to form the daughter-nuclei of each product of division. That attractions and repulsions do exist within the cells is certain; an analysis of their precise nature—the final problem of histology—is still far in the distance. We

cannot get within miles of it. The problem has always loomed before embryologists and histologists,—the historians and mechanicians of the organism. Pander, in the first quarter of this century, was inquiring into the mechanics of development,



Illustrating the Mechanism of Cell-Division,—(*a*) the chromatin elements of the nucleus forming an "equatorial plate" in the lower figure, drawn towards the poles to form two daughter-nuclei in the upper; (*b*) part of the intricate system of fine plasmic threads; (*c*) the centrosomes from which these radiate.—From Boveri.

and Lotze followed him with some luminous suggestions. The task has been continued by numerous modern workers; various "laws of cell-division" have been formulated; many attempts to elucidate the "mechanism" have been made;

but the inquiry is still tentative. The reader may be referred to treatises on the cell by Wilson, Hertwig, and others.

§ 4. *Protoplasmic Restatement.*—In the above helpful suggestion, Spencer has emphasised the reasonableness and general necessity of cell-division at the limit of growth, refraining from the deeper question of the actual mechanism involved. In truth such cautious reserve must still be maintained, but Spencer's analysis perhaps admits of being expressed in lower terms. The early growth of the cell, the increasing bulk of contained protoplasm, the accumulation of nutritive material, correspond to a predominance of protoplasmic processes which are constructive or *anabolic.* The growing disproportion between mass and surface must however imply a relative decrease of anabolism. Yet the life, or general metabolism, continues, and this entails a gradually increasing preponderance of destructive processes, or *katabolism.* As long as growth continues, the algebraic sum of the protoplasmic processes must of course be plus on the side of anabolism, and growth may be now more precisely defined as the outcome of the preponderance of an anabolic tendency, rhythm, or bias. The limit of growth, when waste has overtaken and is beginning to exceed the income or repair, corresponds in the same way to the maximum of katabolic preponderance consistent with life. The limit of growth is the end of the race between anabolism and katabolism, the latter being the winner. Thus cell-division in plants occurs especially at night, when nutrition is at a standstill, and when there is therefore a relative katabolic preponderance.

What is true for the cell, is true for cell-aggregates. Organisms in their entirety have very definite limits of growth. Increase beyond that takes place at a risk, hence giant variations are peculiarly unstable and short-lived. Or again, just as the single cell has found, probably somewhat pathologically, a surface-gaining expedient in the emission of mobile processes, so many organs, notably leaves, have struck a balance between mass and surface by becoming split up into lobes and more or less discontinuous expansions.

Spencer has laid great stress on the importance of the physiological capital with which the organism begins; this represents, in active animals at least, the start which their anabolism gets at the outset. Other things equal, growth varies—(*a*) directly as nutrition; (*b*) directly as the surplus of

nutrition over expenditure; (*c*) directly as the rate at which this surplus increases or decreases; (*d*) directly (in organisms of large expenditure) as the initial bulk; and (*e*) directly as the degree of organisation,—the whole series of variables being finally in close relation to the doctrines of the persistence of matter and conservation of energy. Some apparent exceptions are readily explained. Thus, many plants seem to grow indefinitely, but they expend very little energy, and have often enormous surface area in proportion to mass. The crocodile goes on slowly growing, though at a gradually diminishing rate, but it again expends relatively little energy in proportion to its high nutrition. In many fishes, however, of great activity, the limit of growth seems to be very indefinite. Birds which expend most energy have their size most sharply defined.

§ 5. *The Antithesis between Growth and Multiplication, between Nutrition and Reproduction.*—The life of organisms is conspicuously rhythmic. Plants have their long period of vegetative growth, and then suddenly burst into flower. Animals in their young stages grow rapidly, and as the growth ceases reproduction normally begins. Or again, just as perennial plants are strictly vegetative throughout a great part of the year, but have their stated recurrence of flowers and fruit, so many animals for prolonged periods are virtually asexual, but exhibit periodic returns of a reproductive or sexual tide. Foliage and fruiting, periods of nutrition and crises of reproduction, hunger and love, must be interpreted as life-tides, which will be seen to be but special expressions of the fundamental organic rhythm between sleep and waking, rest and work, upbuilding and expenditure, which are expressed on the protoplasmic plane as anabolism and katabolism.

The common hydra, in abundant nutritive conditions, produces numerous buds, and even these sometimes begin themselves to bear another generation. In other words, we may almost say, with plenty of food the polype *grows* abundantly, so obviously is this asexual reproduction continuous with growth. A check to the nutritive conditions, however, brings on the development of the sexual organs and the occurrence of sexual reproduction. In planarian worms, the asexual multiplication of which we have already noted, Zacharias observed that favourable nutritive conditions were associated with the formation of asexual chains, while a check to the

nutrition brought about both the separation and the sexual maturity of the links. Rywosch corroborates this, noting in *Microstomum lineare* that the generative organs do not become completely matured till the individuals cease to be links in a chain, and that the sexuality is hastened by outside influences such as checked nutrition. The gardener root-prunes his apple-tree, thereby checking nutrition to improve the yield of fruit, in other words, to augment reproduction. Reversely, the removal of reproductive organs may increase the development of the general "body" both in plant and animal,—witness the castrated ox, capon, &c., or the way in which the gardener nips off the flower-buds from his foliage plants. Taking a further step, we recall the familiar and already repeated fact, that favourable nutritive and other conditions enable the aphides to continue parthenogenetic through the summer months; but both for the common plant-lice and for the vine-insect phylloxera, it has been shown that a check to nutrition causes the parthenogenesis to cease, and is associated with the return of sexual reproduction. The above instances are obviously not all upon the same plane. They illustrate however, at different levels, the same great contrast. It is necessary, however, to become more precise.

§ 6. *The Contrast between Growth and Reproduction in the Individual.*—(*a*) *The Distribution of Organs.*—The general position of the flower at the end of the vegetative axis is so obvious a fact that its import tends to be overlooked. The end of the axis is furthest from the source of nutritive supply; with exaggeration, we might call it the starvation-point. There, with katabolic conditions tending relatively to predominate, the reproductive organs are situated. The flower occupies a katabolic position, and is often the plant's dying effort.

In the tiger-lily, growth at first tends to remain continuous, and the base of the bulb bears simple vegetative buds. Further up, however, where nutrition reaches its maximum, the axils of the leaves contain buds, which are separable though still asexual. Finally, further up still, where nutrition is relatively less active and katabolism is maximised, the formation of flowers indicates the appearance of sexual reproduction.

In many ferns, the contrast between the vegetative and reproductive regions of the organism is as marked as in the

flowering-plant. Thus the moonwort (*Botrychium*) and the adder's tongue (*Ophioglossum*) have their spore-bearing shoots standing in conspicuous antithesis to the leafy portion, and a similar contrast is well seen in the royal fern (*Osmunda*) and some of its allies.

In animals, the contrast in position between reproductive organs and the general body is never so marked. Yet the

The Moonwort Fern (*Botrychium lunare*), showing the contrasted frond (*a*), and fructification (*b*).—After Sachs.

Diagram of the Tiger Lily, showing bulbils (*a*) in lower axils, and flower above.

generally posterior position of the organs, their frequent close association with the excretory system, their occasional rupture as external sacs, must not be lost sight of.

(*b*) *The Contrast in the Individual Life.*—Growth during youth, sexual maturity at the limit of growth, the continued alternation of vegetative and reproductive periods, are common-

places of observation which require no emphasis. If growth and vegetative increase are the outcome of preponderant anabolism, reproduction and sexuality as their antitheses must represent the katabolic reaction from these. But anabolism and katabolism are the two sides of protoplasmic life; and the major rhythms of the respective preponderance of these, give the familiar antitheses we have been noting. These contrasts of metabolism represent the swings of the organic see-saw; the periodic contrasts correspond to alternate weightings or lightenings of the two sides. Yet the contrast is less than it seems. In previous chapters we have seen how growth, becoming overgrowth, turns into reproduction; and how sexual reproduction, dispensing with fertilisation, may degenerate till we know it no longer from growth. Reproduction, moreover, is as primitive as nutrition, for not only do hunger and love become indistinguishable in that equal-sided conjugation which has been curiously called "isophagy," but nutrition in turn is nothing more than continual reproduction of the protoplasm. Here, indeed, we have been anticipated by Hatschek, who clearly states the more than verbal paradox, that all nutrition is reproduction.

§ 7. *The Contrast between Asexual and Sexual Reproduction.*—In plenty, the hydra buds; in poverty, it reproduces sexually. In the same way, the liverwort on the flower-pot bears its pretty cryptogamic "flowers" when its exuberant growth and budding have come to an end. On rich soil a plant has luxuriant foliage; but great abundance is the reverse of conducive to the richest crop of flowers and fruit. Gruber, Maupas, and others, have shown that abundant nutrition favours the asexual multiplication, *i.e.*, the division of infusorians. In other words, the maximum size is rapidly reached when food is abundant, but the conditions at the limit of growth bring about reproduction. Preponderant anabolism leads up to the possibility of multiplication, but we need the onset of katabolism to bring about the reproductive crisis. Gruber also notes, that in the very reverse of favourable conditions, rapid division with diminution of size and resulting conjugation sets in; and Khawkine observes the occurrence of division, both at an optimum and in famine. In both cases a katabolic crisis is associated with reproduction, though the crisis may be, and often is, preceded by an anabolic preponderance.

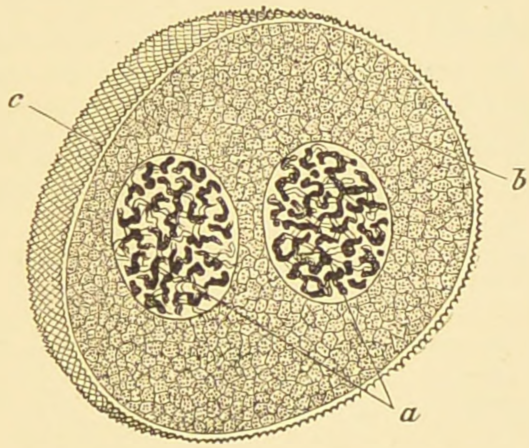
In regard to a common infusorian (*Leucophrys patula*), Maupas observes that with abundant food the ordinary fission continues, but with scanty nutrition a metamorphosis occurs, followed by six successive divisions, which have for their end conjugation. That is to say, we have positive proof that in these lowest organisms, katabolic conditions determine the beginning of sexual reproduction, a matter of no small importance to the evolutionist. Generalising, M. Maupas concludes that the reproductive power of ciliated infusorians depends, (1) on the quality and quantity of the food; (2) on the temperature; (3) on the alimentary adaptation of the buccal organs. He also demonstrates that with a vegetarian diet their rate of asexual reproduction is much less, and the size smaller. Taking these facts, along with his important demonstration that the life of ciliated infusorians runs in cycles of asexual reproduction, necessarily interrupted (if the life of the species is to continue) by conjugation or sexual reproduction, we again reach the general conclusion that anabolic conditions favour asexual reproduction, rather than sexual; and that while preponderant anabolism is the necessary condition of the overgrowth which makes the asexual reproduction possible, the onset of katabolic preponderance is necessary to the act itself.

Semper quotes an interesting observation by Strethill Wright, unfortunately somewhat vague, that certain polyps multiply abundantly in the dark by buds, while in the light, and with insufficient supplies of food, they bring forth sexual individuals or medusæ. More precise is the fact already cited from Zacharias, that the spontaneous asexual multiplication of planarians went on apace when the food supply was copious (anabolic condition), but if the amount of food was reduced or altogether withdrawn (katabolic condition) the asexual reproduction completely ceased. Bergendal reports that in the transverse division of another planarian worm (*Bipalium*), the severed links were all sexually immature; and the results of Rywosch demonstrate the same antithesis between the sexual and the asexual process.

In the same way, sexual reproduction is contrasted with its degenerate expression in parthenogenesis. The conditions of the latter in aphides and phylloxera are demonstrably anabolic, the normal sexual process recurs with the periodic return of hard times, or in relatively katabolic conditions. In the lower crustaceans, a similar contrast of conditions has also been observed.

It is again, on the present view, readily intelligible why in the exceptionally favourable anabolic environment of bacteria and many parasitic fungi sexual reproduction should be absent. Marshall Ward has pointed out that the more intimate the degree of parasitism or saprophytism, the more degenerate the sexual reproduction. The greater the anabolism, in other words, the more growth and the less sexuality. That such comparatively complex organisms can continue their asexual reproduction, dispensing altogether with the acknowledged stimulus of fertilisation, may probably be at least partially explained on the assumption that the abundant waste products of the host act as extrinsic stimuli.

On this view, moreover, alternation of generations loses much of its uniqueness. The contrast between the vegetative



Pollen Grain: *a*, the two nuclei; *b*, the general protoplasm; *c*, the outer wall.—From Carnoy.

asexual hydroid or hydra-tuba, and the active sexual medusoid or jelly-fish, is very marked. So too, on a higher plane, the vegetative spore-producing fern-plant stands opposed to the less nutritive sexual prothallus. The alternation is but a rhythm of large amplitude between anabolic and katabolic preponderance.

What is so marked in the alternation is only a specialisation of the reproductive or sexual parts of the organism as against the growing or asexual ones,—a specialisation which becomes exaggerated into separate existences, each dominated by its own physiological bias.

In the fern or flowering plant the vegetative or asexual existence has preponderated, and this is entirely consistent with the characteristic passivity of plants. This is emphatically

their line of development; but, be it observed, that though in the flowering plants the nutritive generation has dwarfed, and included the sexual, which seem indeed to be mere organs,—the pollen-grain and embryo sac,—yet it is through and for these that we have all the glory of the flower. In animals, with their emphatically active line of development, the reproductive generation is the higher; and in the higher forms the separate asexual existence is wholly lost.

The experiments of Klebs may perhaps be regarded without unfairness as marking the real beginning of a physiology of reproduction in plants. For he has set himself to show how definite environmental conditions of nutrition, temperature, &c., are definitely associated with the occurrence of particular modes of reproduction in Algæ and Fungi. A *Vaucheria*-plant, kept sterile for years, can be made sexual in a few days. A form normally bisexual can be made unisexual. Asexual spore-formation can be induced with certainty by one set of conditions, *e.g.*, in *Hydrodictyon*, and the appearance of sexual gametes by another. Only by definite experiments like these can we pass from vague interpretations to a precise physiology.

SUMMARY.

1. Growth is characteristic of living organisms, though analogous processes occur at the inorganic level. Hunger is an essential characteristic of living matter. As certain as the fact of growth, is the definiteness of its limit alike for cell and for organism in the great majority of cases.

2. Spencer has analysed the limit of growth, in terms of the continual tendency that increase of mass must have to outrun increase of surface.

3. Cell-division at the limit of growth, at the maximum or optimum of size, restores the balance between mass and surface. The actual mechanics of the process are at present beyond analysis.

4. Spencer's analysis may be restated in protoplasmic terms. Growth expresses the preponderance of anabolism; increase of mass, with less rapid increase of nutritive, respiratory, and excretory surface, involves a relative predominance of katabolism. The limit of growth occurs when katabolism has made up upon anabolism, and tends to outstrip it. What is true of the unit, applies also to the entire multicellular organism.

5. Throughout organic life there is a contrast or rhythm between growth and multiplication, between nutrition and reproduction, corresponding to the fundamental organic see-saw between anabolism and katabolism.

6. This contrast may be read in the distribution of organs, in the periods of life, and in the different grades of reproduction. Yet nutrition and reproduction are fundamentally nearly akin.

7. The contrasts between continuous growth and discontinuous multiplication, between asexual and sexual reproduction, between parthenogenesis and sexuality, between alternating generations, are all different expressions of the fundamental antithesis.

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CHAPTER XVII.

THEORY OF REPRODUCTION.

§ 1. *The Essential Fact in Reproduction.*—In the foregoing chapters, the facts involved in the different forms of reproduction have been analysed apart, and separately discussed. Male and female organisms have been interpreted as relatively katabolic and anabolic; the origin of sex, in the individual and in the race, has been traced back to the preponderance of anabolic or katabolic conditions; the ultimate sex-elements were seen to exhibit the same contrast in its most concentrated expression; fertilisation was regarded, not merely as a mingling of hereditary characters, but as a katabolic stimulus to an anabolic cell, and on the other side, of course, as an anabolic renewal to a katabolic cell. Only by a separation of the problem of "sexual reproduction" into its component problems can clearness be reached. Sexual reproduction is like a complex musical chord in the organic life, combining several elements, all of which, however, admit of the same fundamental analysis. Two problems remain,—the psychical aspect of the process; and the import of that common feature of all reproduction, the separation of part of the parent organism to start a fresh life. The latter forms the subject of the present chapter.

§ 2. *Argument from the Beginnings of Reproduction.*—Leconte and others have pointed out that reproduction really begins with the almost mechanical breakage of a unit mass of living matter, which has grown too large for successful co-ordination. Reproduction, in fact, begins as rupture. Large cells beginning to die, save their lives by sacrifice. Reproduction is literally a life-saving against the approach of death. Whether it be almost random rupture or fragmentation, as seen in some of the most primitive Protozoa, or the overflow and separation of multiple buds as in *Arcella*, the organism, which is becoming exhausted, saves itself, and multiplies in reproducing. In some cases, reproduction is effected by

outflowing processes of the cell, which have gone a little too far. Now, such primitive forms of multiplication, gradually becoming more definite, express a relative predominance of katabolism in the unit mass. Reproduction in its simplest forms is associated with a katabolic crisis.

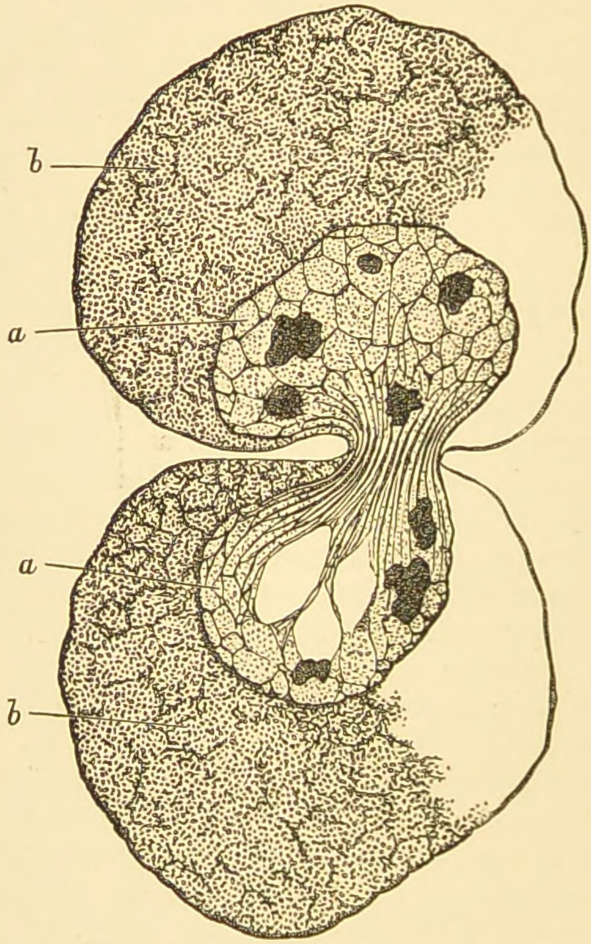
Nägeli's hypothesis as to the origin of reproduction was (in brief outline) as follows:—The original very simple organisms arose from a natural synthesis of albuminoid molecules, a combination of these into micellæ, and a union of these into protoplasts. But the balance between nutrition and expenditure was at first very insecure, and external changes frequently tended to induce latent life, or death. But in the very article of death came the beginning of a new life. Itself too large for coherence, the protoplast broke into parts which lived on, or in other conditions it died down in great part but lived on in a fragment. As differentiation proceeded, the first mode of reproduction by rupture gave place to cell-division, bursting into cells, discharge of special cells; the second gave place to various forms of free-cell formation, spore-building, gemmule forming, &c.

§ 3. *Argument from Cell-Division.*—Most unicellular organisms reproduce by cell-division, and this is, of course, a precedent of reproduction in multicellular organisms, whether they multiply by asexual budding or by differentiated sex-elements. But in the preceding chapter, following Spencer, we have emphasised the connection between division and a katabolic predominance within the cell. A constructive period may precede, but a disruptive climax attends the division. So far then as reproduction is either wholly included in the process of cell-division, or has this as its necessary precedent, it is associated with a katabolic crisis.

§ 4. *Argument from the Gradations between Asexual Severance of Parts and the Liberation of Special Sex-Cells.*—Discussing asexual reproduction, we have noticed that some worm-types break into two or more parts, which start new individuals. That some nemerteans normally break up into pieces, as they do in the feverish anxiety of capture, is most probable; and this is certainly the case in certain annelids. From a syllid, which sets free a sexual individual, the over-growth of an asexual parent, to one which liberates a series of joints, or even a single joint, bearing reproductive elements, is but a slight step. From the last case, to the rupture which liberates sex-elements, is again only a slight advance. A similar series is well illustrated among the Hydromedusæ. The breakage or thinning away which sets a large portion free

is a katabolic process, in a sense a local death. The gentleness of the gradient warrants us in concluding that the liberation of sex-cells, in its earlier expressions at least, is associated with a local or with a general katabolic crisis.

§ 5. *Argument from the Close Connection between Reproduction and Death.*—Without going back to primitive disintegra-



Division of an Animal Cell, showing the nucleus (*a*) in process of forming two daughter-nuclei, showing also the protoplasmic network (*b*).—From Carnoy.

tions, or the asexual severance of more or less large portions, we may point further to the close connection between reproduction and death, even when the former is accomplished by specialised sex-cells. We shall presently discuss at greater length this nemesis of reproduction, but it is important here to emphasise that the organism not unfrequently dies in continuing the life of the species. In some species of the

primitive annelid *Polygordius*, the mature females die in liberating the ova. At a very different level, the gemmules of the common fresh-water sponge are formed in the decay of the asexual adult, while even the sexual summer forms, especially the males, are peculiarly unstable and mortal. The whole history of this form seems a continuous rhythm between life and growth on the one hand, and death and reproduction on the other. Or again, the flowering of phanerogams is often at once the climax of the life and the glory of death. In his ingenious essay on the origin of death, Goette has well shown how closely and necessarily bound together are the two facts of reproduction and death, which may be both described as katabolic crises.

§ 6. *Argument from Environmental Conditions which favour Reproduction.*—The rhythm between nutrition and reproduction, or between growth and multiplication, has been as it were the refrain of the preceding pages. This "organic see-saw" is determined by the very constitution of the organism; in other words, it expresses the fundamental characteristic of living matter. It is an incomplete conception, however, unless it be remembered that about this "organic see-saw" there blows the wind of the environment, swaying it now to one side, now to the other. It is important therefore to illustrate how the play of external conditions accelerates or retards the reproductive function.

The influence of heat upon the reproductive powers of infusorians has been carefully investigated by Maupas. The higher the temperature up to a certain limit, the faster do these organisms reproduce. In favourable nutritive conditions, *Stylonichia pustulata* divides once in twenty-four hours at a temperature of 7° to 10° C., twice at 10° to 15°, thrice at 15° to 20°, four times at 20° to 24°, and five times at 24° to 27° C. Illustrating the rapid rate of increase, Maupas notes in the same paper, that at a temperature of 25° to 26° C., a single *Stylonichia* would in four days have a progeny of a million, in six days of a billion, in seven and a half days of a hundred billions! In six days the family would weigh one kilogramme, and in seven and a half days one hundred kilogrammes.

The action of heat may be twofold; up to a certain limit it quickens development and the general life, favouring asexual reproduction and parthenogenesis rather than the sexual pro-

cess; beyond that limit of comfortable warmth, so variable for different animals, it may induce a feverish habit of body, and hasten reproductive maturity and sexual reproduction. In other words, heat may in some cases favour anabolism, in others katabolism. It is intelligible enough to find increased heat sometimes associated with increased asexual reproduction, sometimes with accelerated sexuality. Instances of both may be gathered from Semper's "Animal Life," the classical work on the influence of the environment upon the organism.

Maupas supplies another vivid illustration of a yet more important environmental influence, that of food. In another ciliated infusorian (*Leucophrys*), so long as food is abundant, fission obtains; but when food grows scanty, there is a metamorphosis without encystation, followed by six successive divisions. These are effected, however, "without vegetative growth, and have for their final object not multiplication but conjugation." In other words, abundant food is associated with asexual reproduction; a check to the nutrition brings about the sexual process. Maupas gives a vivid numerical statement of the stimulus to reproduction by a sudden check to the nutrition. Leucophrys at a temperature of 20° C., in richly nutritive conditions, will give rise to sixteen thousand three hundred and eighty-four individuals in three days; but if the food be then suppressed, this large number will in a few hours be multiplied by sixty-four, resulting in a total of one million forty-eight thousand five hundred and seventy-six individuals!

From cases already cited, which may be multiplied by consulting Semper's "Animal Life," supplemented by a summary of more recent researches by one of ourselves, the general conclusions may be drawn,—(*a*) That heat increases reproduction, either directly or as the result of a preliminary acceleration of growth; (*b*) That increased food will, of course, favour growth, but reproduction may follow all the more markedly as an exaggerated nemesis; (*c*) That checks to nutrition, especially in the form of sudden scarcity, will favour sexual reproduction. The clearest result of all is, that a sudden katabolic change favours reproduction, especially in its sexual form. Anabolic conditions favour reproduction indirectly; the reverse conditions have a direct influence; in both cases, reproduction is the expression of a katabolic crisis.

7. *Conclusion.*—Primitively, then, reproduction was a kata-

bolic rupture of a mass of protoplasm. This becomes more definite in cell-division of various kinds, tending ever to occur at the limit of growth when waste has made up on repair, or in katabolic conditions due to the environment. In multicellular animals, anabolic conditions favour overgrowth; a check to this brings about discontinuous asexual reproduction. With increasing differentiation, the asexual multiplication is replaced by the liberation of special sex-cells, by which the life-saving and life-continuing sacrifice is rendered less costly. Just as asexual reproduction occurs at the limit of growth, so a check to the asexual process is often seen to involve the appearance of the sexual, which is thus still further associated with katabolic preponderance. This is confirmed by the contrasts observed in alternation of generations, where the two processes in varying degrees of distinctness persist in the life-history of the same organism. Corroboration is again afforded by the association of sexual reproduction with sundry environmental checks of a katabolic character. And thus the opposition between nutrition and reproduction, which, after life and death, is the most obvious antithesis in nature, admits of being more precisely restated in the thesis, that as a continued surplus of anabolism involves growth, so a relative preponderance of katabolism necessitates reproduction.

SUMMARY.

1. The essential fact in reproduction is the separation of part of the parent organism to start a fresh life.

2. Reproduction begins with rupture,—a katabolic crisis.

3. Cell-division, which sometimes sums up, and is always associated with, the act of reproduction, occurs at a katabolic crisis.

4. The gradations between discontinuous asexual multiplication and ordinary sexual reproduction, show a lessening of the sacrifice; but all demand a disruption, or a katabolic preponderance.

5. From first to last reproduction is linked to death.

6. Environmental conditions of a katabolic character favour sexual reproduction.

7. General conclusion,—a relative preponderance of katabolism is associated with reproduction, though this may be prepared for by a previous period of predominant anabolism.

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CHAPTER XVIII.

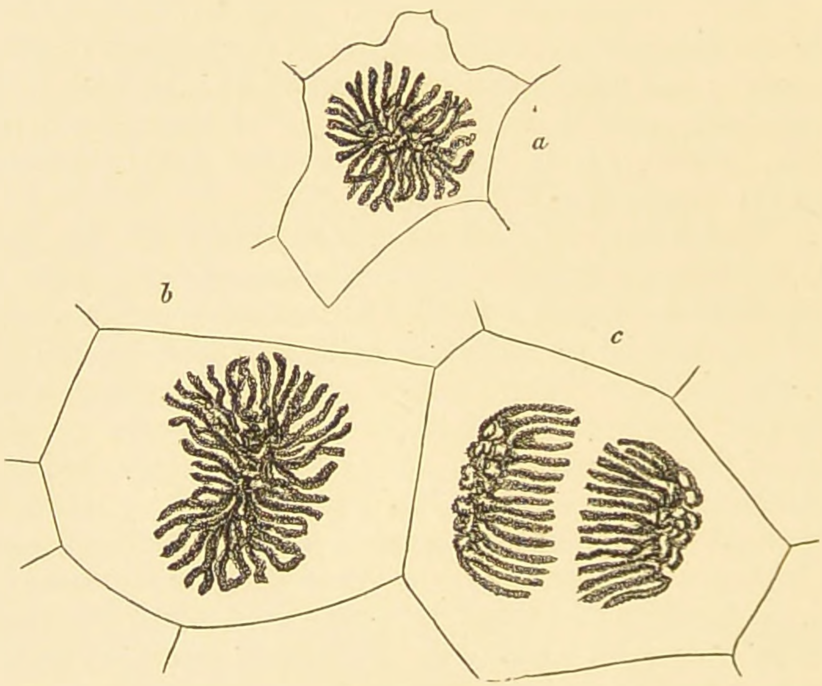
Special Physiology of Sex and Reproduction.

It is no part of our purpose to discuss in detail the physiology of sexual and reproductive functions. The fundamental physiology of the essential functions has been the subject of preceding chapters; the details will be found in the standard works on Physiology, Botany, and Zoology. For the sake of completeness, however, it is necessary to take a brief survey of some of the most outstanding facts.

§ 1. *Weismann's Theory of "Continuity of the Germ-Plasma."*—Thanks, especially to Weismann, the view that ordinary cells of the "body" become at a certain epoch changed into special reproductive cells, may now be put aside as exceedingly improbable. In a minority of cases, already quoted, the reproductive cells, or the rudiments of sexual organs, are demonstrably set apart at an early stage, before the differentiation of the embryo has proceeded far. They thus include some of the original capital of the fertilised parent ovum intact, they continue the protoplasmic tradition unaltered, and, when liberated in turn, they naturally enough develop as the parent ovum did. Following out this important fact, various naturalists have reached the conception of a continuous necklace-like chain of sex-cells from generation to generation,—a continuous chain upon which the mortal individual organisms arise and from which they drop away, like so many separate and successive pendants.

But in the majority of cases, such a conception, as Weismann has justly insisted, gives a false simplicity to the facts. A chain of insulated sex-cells, connecting the parental fertilised ovum with the germ-cells which develop into offspring is, so far as we yet know, only rarely demonstrable. In other words, the rudiments of the reproductive organs often appear at a relatively late stage in the development. Where do they come from? Are somatic, or ordinary body-cells modified

into reproductive elements? Weismann's answer is a decided negative. Although no continuous chain of germ-like *cells* is demonstrable, there is a strict continuity of germ-*plasm*. To quote Weismann's own words, "In each development a portion of the specific germ-plasm which the parental ovum contains, is not used up in the formation of the offspring, but is reserved unchanged to form the germ-cells of the following generation." In short, continuity is kept up by the plasm of nuclei, rather than by a chain of cells. It will be observed, of course, that while early insulation of definite germ-cells is a



The chromatin elements of the nuclei in coil (*a*), double star (*b*), and almost divided stages (*c*).—After Pfitzner.

demonstrable fact, to be seen in a few cases, though perhaps of wider occurrence than we know of, the continuity of germ-plasm is strictly a hypothesis.

This being so, reproductive maturity may be defined as the period when the reproductive cells (bearing the inherited capital of germ-plasm) have established themselves to that degree that they can start fresh organisms, and have multiplied to an extent which in most cases makes their liberation a physiological necessity. In the lower animals, the maturity of the sexual functions is often as slightly marked as the liberation

of the elements is passive and random. In slightly differentiated organisms, like sponges, there is little reason to suppose that the distinction between cells preponderating in germ-plasm and the ordinary cells of the body is much marked. Nor in such cases is the anarchic opposition between body and reproductive cells at all emphatic, especially as regards the female cells. It is only as the differentiation increases, as the contrast between body-cells and sex-cells becomes emphasised, as the asexual mode of getting rid of surplus wanes, that the typical liberation of sex-elements which marks sexual maturity becomes a striking fact in the life. That the male-cells are always more anarchic, usually mature before the female elements, and even in plants, and in such passive animals as a sponge or a hydra, burst from the organism, while the female cells remain *in situ*, is quite consonant with their relatively katabolic character.

§ 2. *Sexual Maturation.*—The maturation of the sexes not only acquires increasing definiteness in the higher forms, but becomes associated with various characteristic accompaniments. The profound reaction of reproductive maturity upon the whole system is best marked in birds and mammals, and perhaps most of all in man. Thus in a young male bird, the circulation in the testes is greatly increased, and these organs increase greatly in size and weight, and commence to develop spermatozoa. Meanwhile the "secondary sexual characters" of the adult—gayer plumage possibly attractive to the female, or weapons for contest with other males—appear, the voice and note may alter, and a marked increase of strength and courage may occur. Among mammals, the changes are of similar order, the secondary sexual characters of course differing in detail. The minor changes at puberty in man associated with the commencement of spermatogenesis, are (besides the reflex excitation of erection due to distension of the seminal vesicles, and the more or less periodic expulsion of their contents during sleep) the growth of hair on the pubic region and later on the lower part of the face, and the rapid modification of the laryngeal cartilages and the lengthening of the vocal chords, so rendering the voice harsh and broken during the change, and ultimately deepening it by about an octave. The marked strengthening of bones and muscles, and the profound psychical changes which accompany the whole series of processes, are also familiar.

Although we do not understand the facts, there is no doubt as to the profound correlation which exists between the reproductive organs and the body. This may be illustrated in various ways, *e.g.*, by reference to the effects of castration. On young cocks, according to Sellheim, this operation has very diverse results, sometimes decreasing the secondary sex-characters, and sometimes, strange to say, increasing them. The capons seldom crow, or do so abnormally; attempts at copulation are rare. But one general result seems to be established, that the whole body is affected:—the larynx is intermediate in size between that of cock and hen; the syrinx is weakly developed; fat accumulates in the connective tissue; the brain and heart are light in weight; even the skeleton shows many abnormalities. ("Beiträge zur Geburtshilfe und Gynäkologie," i., 1898, pp. 229-246.) The same investigator has also shown that in mammals of both sexes the removal of the reproductive organs markedly prolongs the period of bone-development, and has thus an effect on the shape of various parts. (*Op. cit.*, ii., 1899, pp. 236-59.)

In regard to the correlation of antlers and reproductive organs ("Arch. Entwickmech.," viii., 1899, pp. 382-447), A. Rörig has investigated five points. His first question is: Does the absence of antlers or the development of only one depend on an abnormality of the reproductive system? He answers that the condition may occur with both normal and abnormal gonads. His second question is: Can the occasional development of antlers in female Cervidæ be referred to the abnormal development of the reproductive organs? He answers that a diseased state on one side may be correlated with the development of one antler, on both sides with the development of two antlers, and that one-sided disease has a correlation operating transversely. If the ovaries are atrophied there are usually antlers. Hermaphrodites seem always to have antlers, and these are the more perfect the more the gonads incline towards maleness. Irritation of the appropriate place may also evoke antlers in females. His third question is: What effect has partial or total castration in the males? It is answered that the effect varies according to the age of the animal and the stage of antler development. In a young quite hornless male, castration entirely inhibits the growth of antlers. Fourthly, Rörig points out that atrophy of the testes is followed almost always by the formation of "Perücken"-antlers, and injury to the testes by premature casting. Fifthly, the excision of the antlers has no deleterious effect on the reproductivity or health of the individual. It is obvious that this is a very important contribution to our knowledge of the correlation between gonads and soma.

In higher vertebrates, the sexual maturity of the female is marked by a cellular activity within the ovary, not less remarkable than that in the testes. Associated therewith are minor but often very important characteristics, such as the increased mammary development in mammalia. In some of the lower animals, such as certain marine annelids, the ova become so numerous that their disruption or liberation is in great part a mechanical necessity. The same might be said of fishes, reptiles, and birds. At the same time the enlargement and

escape of the ova are doubtless expressions of a normal cellular rhythm, of which hints are given in the frequent passage from an amœboid to an encysted phase, in the occasional relapse to the former, and in the fatty degeneration or death of ova which have not accomplished their destiny.

The primitive ova of vertebrates lie in clusters in the substance or stroma of the organ, and are produced from the essential germinal epithelium. Only a minority, however, grow into genuine ova; others, of smaller size, form a nutritive sheath or follicle around them. In mammals, each follicle forms a cavity containing a fluid. Into this the ovum, surrounded by a mass of follicle cells, projects. When mature, the follicle with its contained ovum has attained a superficial position. By the bursting of the ripe follicle the ovum is expelled, and passes into the approximated and ciliated upper end of the oviduct or Fallopian tube. The rupture of blood-vessels in the substance of the ovary fills up the Graafian follicle with blood. The white corpuscles form a framework resembling connective tissue, in which the solids and corpuscles of the blood serum, with colouring matter derived from the hæmoglobin of the latter, are retained. The whole constitutes the "corpus luteum," which, should pregnancy occur, may persist and undergo further retrogressive changes, or otherwise gradually disappear.

As to the direct causes of this process of ovulation there is some difference of opinion. The congestion of the blood-vessels of the ovary, its own internal turgidity, a slight contractility of its stroma, have been regarded as determining factors. The process seems, however, rather to depend upon the growth and turgescence of the individual follicle. The question of the relation of ovulation to the process of copulation in the higher animals has also been much discussed. Though we certainly know that ovulation is of regular occurrence whether fecundation takes place or not, it seems that in many cases copulation is speedily followed by the liberation of an ovum; nor is it difficult to see how the profound nervous and circulatory excitement associated with the former process might accelerate the bursting of a follicle. Leopold has conclusively shown, however, that ovulation may also long precede impregnation, and Stratz has shown, in the case of *Tupaia javanica*, that after fertilisation of ova shed into the oviduct, the follicles in the ovary undergo degeneration, and no more mature eggs are formed till near the end of pregnancy ("Die Geschlechtsreife Saügethierstock." Haag, 1898, pp. 67, 9 pls.). The experiments of Heape ("Proc. Roy. Soc.," lxi., 1897, pp. 52-63) and others show that artificial insemination may be effective in certain mammals, such as mice and dogs; on the other hand, Heape's observations on the rabbit point to the conclusion that both copulation and the presence of spermatozoa in the uterus are necessary to induce ovulation in the virgin rabbit when she is in "heat."

Since the oviduct, unlike its male counterpart, is not, in the vast majority of vertebrates, continuous with its associated organ, it is often difficult to see how the ova once liberated into the body-cavity find their way safely into the small opening of the duct. The problem has been worked out by Nussbaum in the frog, where the ova are moved by the effective action of numerous muscles and by the ciliary activity of peritoneal

epithelial cells which are disposed in tracts converging to the oviducal aperture, so propelling the ova in the right direction. In reptiles, birds, and mammals the open end of the oviduct is widened, fringed, and ciliated, and lies close to or even touching the ovary; muscular fibres too are present, and more or less active movements of this ciliated end over the ovarian surface have been alleged to occur. The oviduct once reached, the downward progress of the ovum is ensured by the cilia of the epithelial lining, and probably also by peristaltic movements of its muscular coat.

There is no doubt that the advent of sexual maturity varies with environmental conditions of climate, food, and the like. Broadly speaking, sexuality becomes pronounced as growth ceases. Especially in higher organisms, a distinction must obviously be drawn between the period at which it is possible for males and females to unite in fertile sexual union, and the period at which such union will naturally occur or will result in the fittest offspring. In the lower animals, where the individual life is usually shorter, sexual maturity is more rapidly attained, though we find cases such as that of the fluke (*Polystomum*) so commonly present in the bladder of the frog, where maturity of the reproductive organs does not occur for several (three) years, and maturity of growth for some years afterwards. In cestode parasites, the bladder-worm stage remains indefinitely asexual until in fact the stimulus of a new host admits of the development of the sexual tapeworm. In plants, reproductive maturity sets in at various ages; thus we have all gradations, at the one extreme our characteristically short-lived but magnificent annuals, then the biennials, and from these to a maturation at still longer date, as in the well-known case of the American aloe (*Aloe americana*), which even in Mexico takes from seven to twelve years to reach the floral climax in which it expires, and in our greenhouses as much as a generation or two, whence its name of "century plant."

In contrast to such cases, precocious reproductive maturity occasionally occurs. We have already referred to those dipterous midges (*Cecidomyia*), in which the larvæ for successive generations become reproductive, though only parthenogenetically. Very striking too is the trematode worm *Gyrodactylus*, which recalls the mystical views of the preformationists, in exhibiting three generations of embryos, one within the other, while the oldest is yet unborn. The well-known axolotl of Mexican lakes, though with its persistent gills in a sense the larval form of *Amblystoma*, attains of course to sexual maturity. A more marked precocity has been observed in the

Alpine salamander (*Triton alpestris*). In higher organisms, it occasionally happens that long before growth has ceased or adolescence been reached sexuality sets in, especially in the male sex, but this is fortunately a comparatively rare pathological occurrence. In one set of organisms precocious reproductive maturity has been of paramount importance, viz., in the flowering plants. Here the prothallus stage, as contrasted with the vegetative, has been much reduced, and has remained associated with or been absorbed by the asexual generation. This is to be in part explained by the accelerated reproduction of the prothallus, comparable to a similar process which has reduced the separate medusoid sexual persons of a hydroid colony to mere buds.

It would be interesting to consider in this connection the profound changes of *habit* often associated with reproductive maturity, but in most cases the facts are inadequately known. It has been often said that it is a *nisus generativus* which prompts the salmon to leave the sea where it feeds and to pass up the rivers where it reproduces, but it must be noted that salmon are seen ascending the rivers throughout the whole year in all stages of reproductive development (D. Noel Paton, Report on Life History of Salmon. Fishery Board for Scotland, 1898). It has been often said that it is a *nisus generativus* which prompts the migratory birds to fly in spring from the warmer areas where they winter to the colder areas where they breed, and it is admitted that the adult males are the first to leave, but the difficulty remains that a large proportion of the migrants are in most cases immature, and do not breed in that season.

§ 3. *Menstruation.*—The process of menstruation (*menses*, *catamenia*), although from the earliest times the subject of medical inquiry, is by no means yet clearly understood. It occurs usually at intervals of a lunar month in all women during their period of potential fertility (fecundity), and is not confined to the human species, having been observed in a number of mammals, *e.g.*, some monkeys (*Macacus rhesus*, *Semnopithecus entellus*), the lemur *Tarsius*, *Tupaia javanica*, and the common shrew (in the last case without proof of outflow of blood). See W. Heape, "Proc. Roy. Soc., London," lx., pp. 202-205.

Though thus clearly a normal physiological process, it yet evidently lies on the borders of pathological change, as is evidenced not only by the pain which so frequently accompanies it, and the local and constitutional disorders which so frequently arise in this connection, but by the general systemic disturbance and local histological changes of which the discharge is merely the outward expression and result. In general terms, and apart from

ovulation, menstruation may be described as a periodic discharge of blood, glandular secretion, and cellular detritus from the lining of the uterus. After from three to six days the blood ceases to appear, and the lost epithelium is rapidly replaced, apparently by proliferation from the necks of the glands. By the ninth or tenth day the mucous coat is fully healed, and the beginnings of the next menstrual process recommence.

The age at which the process commences varies with race and climate, with nutrition and growth, with habit of life (*e.g.*, with difference between town and country life), and with mental and moral characteristics. Of these, however, climate seems most important; thus, while in Northern Europe the age is reckoned at the beginning of the fifteenth year, in the tropics it commences earlier, in the ninth or tenth year, according to some. The cessation of menstruation usually takes place between the age of forty-five and fifty, and, somewhat as the secondary characteristics of female puberty coincide with its appearance, a less distinct reduction of these is associated with its close; in many cases secondary resemblances to the masculine type may supervene.

The old theories of menstruation were, that it served to rid the system of impure blood, that it simply corresponded to the period of "heat" observed in lower animals, or, later, that it was associated with ovulation,—which indeed seems broadly to correspond with the end of the menstrual period. In *Tupaia*, Stratz has shown that the eggs are mature at the beginning of menstruation, and ready for fertilisation at its end. And while it cannot be maintained that either "heat" or ovulation are *necessarily* associated with menstruation in *Homo*, there can be little doubt of the general physiological parallelism of all three processes. At present there may be said to be two rival theories. According to the first of these, the process is viewed as a kind of surgical "freshening" of the uterus for the reception of the ovum, whereby the latter during the healing process can be attached safely to the uterine wall. The other view is exactly the reverse of this. Its upholders regard the growth of the mucous coat before this commencement of the flow as a preparation for the reception of an ovum if duly fertilised, and the menstrual process itself as the expression of the failure of these preparations,—in short, as a consequence of the non-occurrence of pregnancy. A decided majority of gynæcologists appear to incline to the latter view.

The process may, however, be expressed in more general, and at the same time more fundamental terms. If the female sex be indeed preponderatingly anabolic, we should expect this to show itself in distinctive functions. Menstruation is one of these, and is interpretable as a means of getting rid of the anabolic surplus, in absence of its consumption by the development of offspring,—just as it is intelligible that the process should stop after fertilisation, when replaced by the demands of the practically parasitic fœtus. In the same way, the occurrence of lactation, after this internal parasitism has been terminated by birth, is seen to be reasonable. The young mammal is thus enabled to become what is practically a temporary ecto-parasite upon the unfailing maternal anabolic surplus; and when lactation finally ceases, we have the return of menstruation, from which the whole cycle may start anew. So in the widely different yet deeply similar world of flowers, the distinctly anabolic overflow of nectar ceases at fertilisation, and the surplus of continued preponderant anabolism is drafted into the growing seed or fruit.

§ 4. *Sexual Union.*—In a previous chapter we have noted the passive and random way in which the sex-elements of many of the lower animals are liberated, and the chance manner in which they are often brought together by water-currents and the like, though this may not be quite so common as our ignorance leads us to suppose, witness the alleged occurrence of sexual union in *Asterina* and *Antedon.* Yet more in plants is the liberation of male elements, and notably that of pollen-grains, a passive dehiscence, and fertilisation a matter of chance, only reduced by the prodigal wealth of material. Secure as the methods of fertilisation of flowers by the aid of insects often are, the margin of risk is wide; and this is yet more marked when the pollen is carried by the wind. It is true that, both in plants and animals, there are subtle attractions between the essential elements, but this is only at a close range; and the external union is in many cases none the less random.

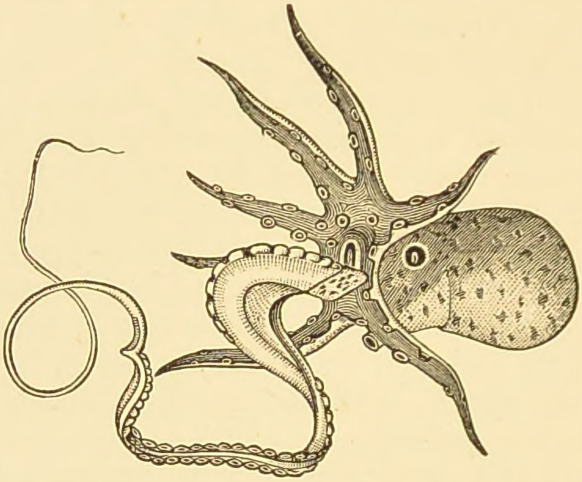
It is important to keep clearly in mind the different forms of sexual relation which may occur. There may be mating at random within the limits of the race ("pangamic" mating), or there may be casual mating between members of different races, or there may be some form of selective or preferential mating within a race. Various forms of the latter may be distinguished (following Pearson's classification and terminology)—

(*a*) Autogamic, or self-fertilisation.
(*b*) Endogamic, within the family, brood, or clan.
(*c*) Homogamic or assortative, or the mating of like with like, the two mates not being of the same breed, or not necessarily so.
(*d*) Preferential or apolegamic—*i.e.*, with sexual selection in the narrower sense of Darwin.
(*e*) Heterogamic, or the mating of unlikes. (See Pearson's "Grammar of Science," 2nd ed., pp. 423-424.)

As it is essential that there should be a timely encounter of the ovum and spermatozoon, we naturally find a very varied series of adaptations securing fecundation. And while the physical adaptations are important, we have also to recognise that the increasing differentiation of the sexes has in the higher animals been enhanced by psychical as well as physical attractions, thus more and more ensuring the continuance of the species.

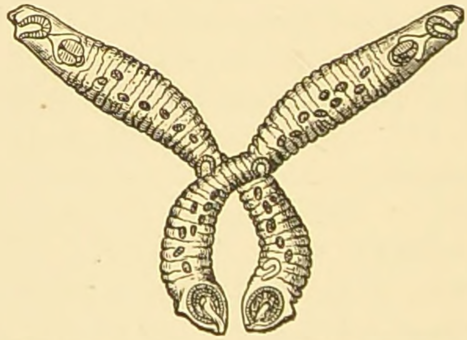
A not unfrequent mode of fecundation is by means of spermatophores, or packets of spermatozoa. These may be seen at times attached to the earth-worm, or found within the leech and snail. Even in newts spermatophores may be formed, and taken up as such by the females.

In the spider the spermatozoa are stored in a special receptacle on the



Male of Paper Nautilus (*Argonauta*), with its modified arm.—From Leunis.

palp, and hence hastily transferred to the fierce female. In cuttlefishes this mode of impregnation is yet more marked. One of the "arms" of the male, much modified and laden with spermatophores, is thrust, or in many cases bodily discharged into the branchial cavity of the female, where it bursts. Such a discharged arm was, on first discovery, regarded as a



Diplozoon paradoxum, a double organism formed from the union of two distinct hermaphrodite individual trematodes (*Diporpa*) at an early stage in their life.

parasite, and hence received the name of Hectocotylus. A curious aberration from the ordinary relations is figured above, where two distinct individuals of a species of fluke (*Diplozoon*) join in almost life-long union.

In many cases again, especially in bony fishes, there is a sexual attraction between male and female, but without any copulation. The female, accompanied by her mate, deposits ova, which he thereupon

fertilises with spermatozoa. A slightly more advanced stage is seen in the frog. Fertilisation is still outside the body of the mother, but the male, embracing the female, liberates spermatozoa upon the eggs, just as these are laid.

In the majority of cases, however, special organs for emitting and for receiving spermatozoa are developed, and copulation occurs. The male organ is often an adaptation of some structure already existing, as in many crustaceans, where modified appendages form external canals for the seminal fluid. In skates and other gristly fishes, the remarkably complex copulatory organs, the so-called "claspers," are in close connection with the hind limb. The penis of higher vertebrates is virtually a new organ. The copulation may be quite external, as in crayfishes, &c., where the male, seizing the female, deposits spermatozoa upon the already laid eggs. Oftener, however, it is internal, and the intromittent organ is inserted into the genital aperture of the female. True copulation may occur without the presence of special organs,—notably in the case of many birds, where the cloaca of the male is apposed to that of the female. The spermatozoa, forcibly expelled by the excited male organs, pass up the female ducts, probably, in part, as the result of peristalsis, but chiefly at least by their own locomotor energy, and one of them may eventually fertilise an ovum. In addition to the intromittent organ, and the lower portion of the female duct which receives it during copulation, there may be auxiliary structures, such as true claspers for retaining hold of the females. The limy "cupid's dart" or "spiculum amoris" of the snail, is usually interpreted as a preliminary excitant.

Three further notes in regard to higher animals are requisite. (1.) There is much reason to believe that the follicles tend to burst towards the end of menstruation; that this may be accelerated by copulation; successful fertilisation may occur at any period, but most frequently soon after menstruation, and most rarely during the relatively infertile period most distant from that process. (2.) After conception, when the fertilised egg has begun to develop, the mouth of the uterus is closed by a secretion, which prevents the entrance of other spermatozoa should further copulation occur. (3.) The period of gestation—*i.e.*, between the fertilisation of the ovum and the extrusion of the fœtus, varies widely in mammals, from about 18 days in opossum, or 30 in rabbit, to about 280 days in Homo or 600 in the elephant, being longer in the more highly evolved types. But the length of the period should also be considered in relation to size, being about 280 days in cow and 150 in sheep; in relation to number of offspring, being about 350 in mare and 60 in dog; and in relation to the degree of maturity at birth, being 420 in giraffe and 40 in kangaroo.

§ 5. *Parturition.*—In many cases—*e.g.*, marine annelids, mature ova burst, as we have already noted, from the mother animal, who may thenceforth have nothing more to do with them. Liberation of ova from the ovary and from the organism may be almost coincident, as in most bony fishes. In other cases, the ova are retained within the mother until fertilised, but are expelled not long after, before development has advanced to any marked degree. Such eggs are often

furnished with the important capital of nutriment, so familiar in the case of birds, and may be also surrounded by chitinous, horny, membranous, or limy shells. All such forms of birth are familiarly described as *oviparous*.

In numerous invertebrates, fishes, amphibians, and reptiles, the ova develop within the mother, and the young are born more or less actively alive. To such cases, where there is no nutritive connection between parent and offspring, the term *ovo-viviparous* used to be applied. They were contrasted with oviparous birth, as in birds, on the one hand, and with the viviparous birth of mammals, on the other. It is the well-known characteristic of the latter that there is an intimate nutritive connection between mother and offspring. The term is of little use, however, for the cases to which it is applied shade off towards the two other forms of birth. Thus among gristly fishes (*Mustelus lævis* and *Carcharias*), in the curious bony fish *Anableps*, and in certain lizards (*Trachydosaurus* and *Cyclodus*), a somewhat placenta-like function is discharged by the yolk-sac and the wall of the oviduct; while in fishes, reptiles, &c., oviparous and ovo-viviparous birth may occur in nearly related forms. The distinction involved in the term is therefore abandoned, and it must also be recognised that the difference between egg-laying and the production of young actively alive is only one of degree. Even in mammals, which are viviparous *par excellence*, the two lowest genera—the duck-mole and the Echidna—are oviparous. The common grass-snake, normally oviparous, has been induced, in artificial conditions, to bring forth its young alive, and this is probably true of other forms. The parthenogenetic generations of aphides are usually viviparous, while the fertilised eggs are laid as such.

Beard has maintained that there is a definite stage in development when the embryo first begins to put on its specific characters, and calls this the critical stage. He believes that in the early days of mammalian evolution, before an allantoic placenta had arisen, the birth period and the critical period (on to the critical stage) coincided; and this is still seen in several marsupials. Then, too, the ovulation period must have been almost equal to—really a little longer than—the critical period, for a coming ovulation, with its reflex message from ovary to uterus, was the direct cause of birth. In higher mammals, the evolution of an allantoic placenta provided for

the nutrition of the fœtus beyond the critical period, or, more technically, beyond a single "critical unit." But the interesting fact is that a correspondence between the length of gestation and a certain number of critical and ovulation units (up to eight) is still preserved. The critical period, multiples of this, and the ovulation periods, must very frequently be times of abortion in mammals; and menstruation is comparable to an abortion prior to a new ovulation. There are no doubt difficulties connected with this theory, and Beard ingeniously deals with some of these, but the idea is a luminous one that the span of gestation, the ovulation period, and the critical unit are all connected as expressions of the rhythm of reproduction in mammals,—a rhythm which has its basis in the ovary. By ovulation the rhythm is proclaimed throughout the reproductive life of the female; in gestation the same rhythm is maintained but in a modified fashion; and as the span of uterine life draws to a close, it again asserts itself, and induces birth. "Thus harmony and law reign in the reproductive life of Mammalia."

§ 6. *Early Nutrition.*—The early nutrition of the embryo, and even larva, is in most cases an absorption of the legacy of yolk material, which is probably richest in the eggs of birds. The tadpole of the frog grows and exerts itself for a short time at the expense of its legacy; it then begins to feed for itself, but it is interesting to notice that before metamorphosis is accomplished the growth of new structures appears to be provided for by the nutritive absorption of the tail, the larva literally living upon itself. The same is true in the elaborate metamorphosis of echinoderm larvæ. In many cases, the cells of the embryo, independently and actively, devour the yolk and other available material, after the amœboid fashion technically known as intra-cellular. At the same time, osmotic currents may more passively effect the like result.

In the buckie or whelk (*Buccinum undatum*) the eggs are enclosed in capsules secreted from the sole-gland of the foot, and the early nutrition is remarkable: a cannibalism occurs among the crowd of embryos enclosed within each capsule. The stronger and older devour the younger and weaker,—a struggle for existence happily of exceptional precociousness.

The conception of a struggle for existence applies to the earliest chapters of life. There is struggle among potential ova, and struggle amid the crowd of spermatozoa; there is

struggle between embryo and mother, and struggle between adjacent embryos. Thus De Bruyne notes in regard to fresh-water mussels, the struggle between the successful ova and the adjacent cells, and the continuance of this between the embryos and the maternal leucocytes, and even on to the time when the larvæ are temporarily parasitic in the skin of a fish. (See "Arch. Biol.," xv., 1898, pp. 181-300, 5 plates.)

In the higher vertebrates (above amphibians), two fœtal membranes—amnion and allantois—are developed, in addition to the yolk-sac which encloses the yolk. Of these the amnion is mainly protective, and the allantois at first almost wholly respiratory. But in birds (and to a slight extent in some reptiles) the allantois begins to assume nutritive functions, assisting in the absorption of the yolk. In placental mammals this nutritive function becomes paramount, the allantois forming the greater part of the embryonic side of the placenta. The yolk-sac is here virtually yolk-less, but in some forms it serves for a time to absorb nutriment as it did in birds, though from a different source,—the maternal wall. In most cases, however, what was incipient on the part of the yolk-sac in the exceptional elasmobranchs and lizards already mentioned, becomes the emphatic function of the allantois,—namely, the establishment of a vascular or nutritive connection with the wall of the maternal uterus. By this means a very intimate osmotic transfusion is effected.

§ 7. *Lactation.*—If menstruation be a means of getting rid of anabolic surplus, in absence of the fœtal consumption, lactation is still more an anabolic overflow, adapted to, though not of course originally caused by the offspring's demands. It is at the same time evident enough, and easily verified by the histologist, that in actual occurrence both processes are katabolic, involving cellular disruption and death. That peculiar liability of these uterine and mammary tissues to disease, which furnishes the most tragic possibilities of the life of woman, becomes thus less mysterious. We can understand more readily the association of such diseases with much of what we are pleased to generalise as civilisation, and view more hopefully the possibilities of their enormous diminution by the rational hygiene of civilisation properly so called.

The milk or mammary organs are modified skin-glands, probably most nearly allied to the ordinary sebaceous type, except in monotremes, where they seem to be allied rather to

the sweat glands. Every one knows that they are exclusively characteristic of mammals, and are only normally functional in the female sex. Rudimentary in the males, they may even there produce milk ("witches' milk") at birth, puberty, and under pathological conditions, while cases have been put on record of males who have actually given suck. Merriam (Hayden's U.S. Geol. Survey, VI., p. 666) gives a definite account of male lactation in *Lepus bairdi.* They vary greatly in position and number, a large number being doubtless the primitive condition. It has also been shown that the nuclei of the gland cells undergo degeneration, disruption, and expulsion, and they, in all likelihood, form the casein elements of the nutritive fluid. Some of the abundant leucocytes or white blood corpuscles also migrate through the epithelium, but it is not proved that they actually share in forming the milk, though they may bring fat globules into it. (See L. Michaelis, "Arch. Mikr. Anat.," li., 1898, pp. 711-747, 2 pls.)

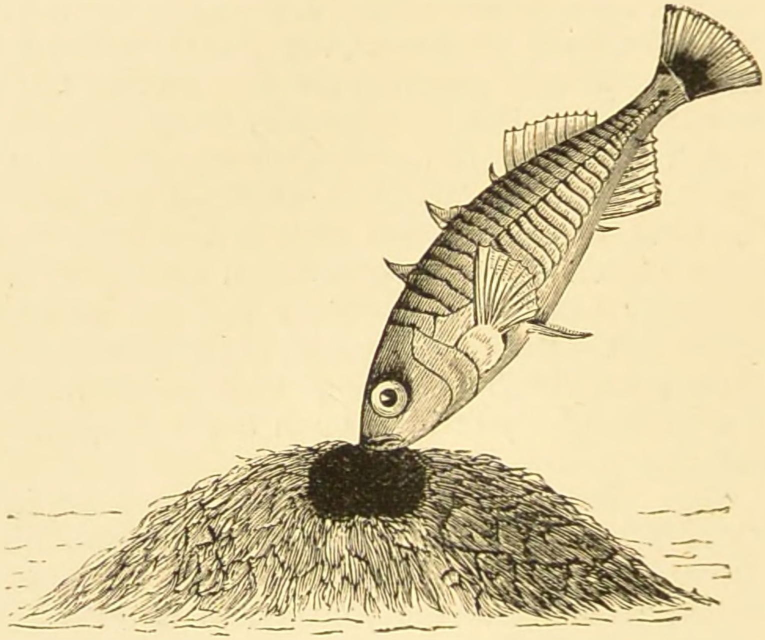
Before birth, the mammalian embryo has been nourished through the placenta, by the transfusion already referred to. The alimentary canal has obviously had no experience in digestive function. Before it proceeds to digest the food of the parents, it is put through a course of what Sollas neatly terms "gastric education," by feeding upon the readily assimilated mother's milk.

§ 8. *Other Secretions.*—Every one has at least heard of "pigeon's milk," and many are familiar with its administration to the young birds. It is produced by both sexes, especially just after the hatching of the young, and is the result of a degeneration of the cells lining the crop. Some of the cells break up, others are discharged bodily. The result forms a milky emulsion-like fluid, which is regurgitated by the parents into the mouth of the young bird. A similar substance is said to occur in some parrots.

Of some interest also is the supra-salivation which occurs at the breeding season in the swiftlets (*Collocalia*), which form the edible birds' nests, the costly, though to us wofully insipid, luxury of Chinese epicures. Certain salivary glands become peculiarly active in these birds when breeding, and the secretion, which, according to Green, consists chiefly of a substance akin to mucin, is used to form the snow-white fibrous nest.

Take only one other instance of peculiar secretion, curiously linked to the above by one of those profound physiological

unities which show how superficial after all are the utmost contrasts of organic form,—we refer to the viscid threads with which the male stickleback weaves his nest. Möbius has shown that the kidneys are greatly affected by the growth of the testes; that they produce, by a semi-pathological process, special waste or katabolic elements, in the form of mucous threads. The male gets rid of this uneasy encumbrance (which has a somewhat parallel pathological equivalent in higher animals), by rubbing itself against objects, and thus almost mechanically has been evolved the familiar weaving of the aquatic nest.

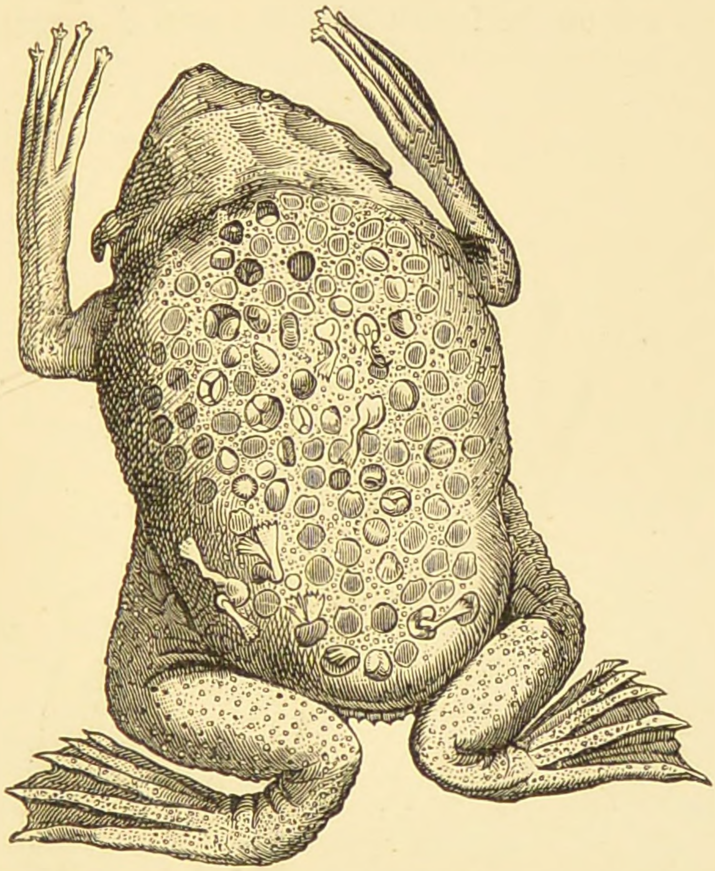


The Nest of the Stickleback (*Gasterosteus*).—From Thomas Bolton

§ 9. *Incubation.*—The physiological sacrifice of the female birds does not end with providing the large capital of nutritive material with which the germ is endowed, but is continued in all the patience of brooding. In passerine birds the male relieves the female in her task of love, and in the ostrich and *Rhea* he plays a prominent part. In the cuckoos and cow-birds the parental care is shirked, and with varying degrees of deliberateness the eggs are foisted into foster nests, and the young thus put out to nurse. After the fatigue of reproduction it is perhaps natural enough that the female should rest awhile upon the eggs in the shelter of the nest, and since there is

observed to be an increased circulation in the skin of the abdominal region at this time, it has been argued that the bird merely sits to cool itself! Primitively, the incubatory instinct may be traced back to the need for rest, as a reaction after the fatigue of reproduction.

Here too one must include the retention of the young in skin pouches, exhibited by the great majority of marsupial mammals and by the Echidna. In the latter, the pouch is a

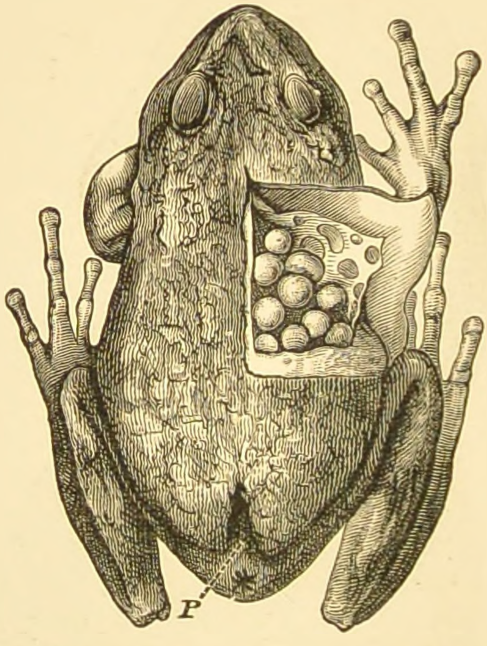


The female Surinam Toad, with young ones on its back.—From Leunis.

simple and possibly periodic structure, arising from an insinking of the skin in the mammary region of the abdomen. Here the eggs are somehow or other stowed away and the young developed. The milk glands simply open on the surface of the depression. In most marsupials, the young, which are born precociously after a very short uterine life, are sheltered in similar, but more developed, pouches of the skin, within which the teats open.

In oviparous reptiles, the eggs are usually left to hatch of themselves, aided by the warmth of sun and soil. "The female python disposes herself in coils round her eggs, and incubates them for a prolonged period, during which the temperature has been observed to rise as high as 96° F. within the coils."

Some exceedingly curious parental adaptations occur among amphibians, which seem to have made numerous experiments in this direction. Thus in the Surinam toad (*Pipa*), the male spreads the ova on the female's back, a sort of erysipelas sets



The female *Nototrema marsupiatum*,—an amphibian, with eggs in a dorsal sac, which is shown partly uncovered. —From Carus Sterne, after Günther.

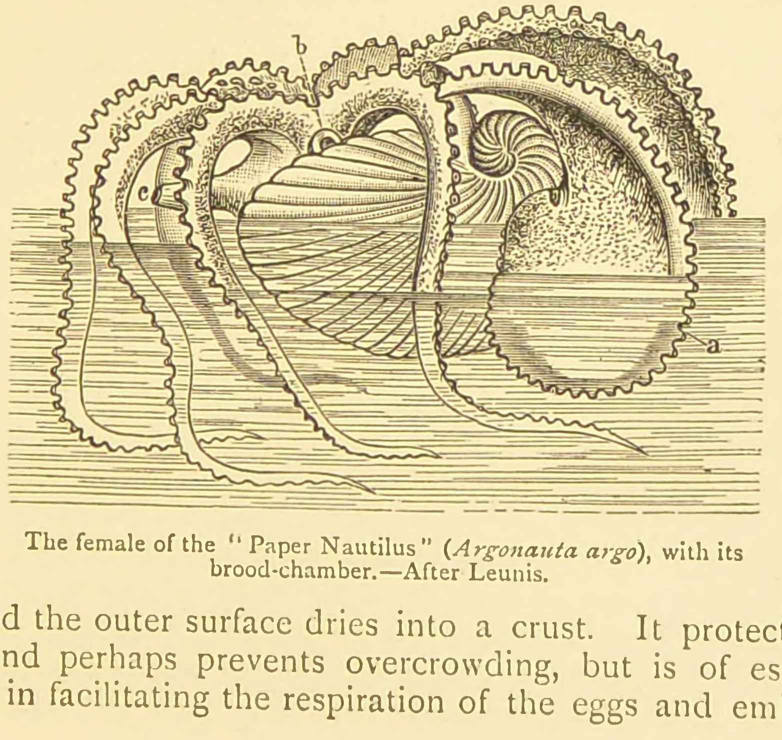
in, and each ovum becomes surrounded by a skin-cavity in which the tadpole develops. After the process is over, the skin of the back is renewed. In other cases this mode of carrying the ova becomes somewhat more definite; thus in *Notodelphys* and *Nototrema* the eggs are stored in dorsal pouches. Nor are the males without their share in the task of parentage. In the obstetric frog (*Alytes obstetricans*), the male helps to remove the eggs from the female, twists them in strings round his hind legs, and buries himself in the water till the tadpoles escape and relieve him of his burden. In *Rhino-*

derma darwinii, the croaking sacs, which were previously used for amatory calling, become enlarged as cradles for the young.

In a Japanese tree-frog (*Rhacophorus schlegelii*) the female

The Sea-horse (*Hippocampus guttulatus*).—From the Atlas of the Naples Aquarium.

lays the eggs in a hole in the mud, and by curious kneading and treading movements works the jelly which surrounds them into a froth. The frothy envelope is like well-beaten white of



The female of the "Paper Nautilus" (*Argonauta argo*), with its brood-chamber.—After Leunis.

egg, and the outer surface dries into a crust. It protects the eggs, and perhaps prevents overcrowding, but is of especial service in facilitating the respiration of the eggs and embryos.

(S. Ikeda, "Annot. Zool. Japon.," i., 1897, pp. 113-122, 2 figs.)

Among fishes, parental care is largely in abeyance, and there are only slight hints of anything in the way of incubation. In a siluroid fish (*Aspredo*), the female deposits her ova and lies upon them till they become attached to the spongy skin of the belly, very much as happens in the dorsal attachment of the Surinam toad. After hatching, the skin excrescence is smoothed away. In *Solenostoma* (allied to pipe-fish) the ventral fins unite with the skin to form a pouch in which the eggs are retained. In other cases, it is the male which incubates or cares for the ova. Not a few form nests, as in the stickleback, over which they keep a jealous guard. In some species of *Arius* the eggs are carried about in the pharynx; while in the sea-horses a pouch is developed on the posterior abdomen.

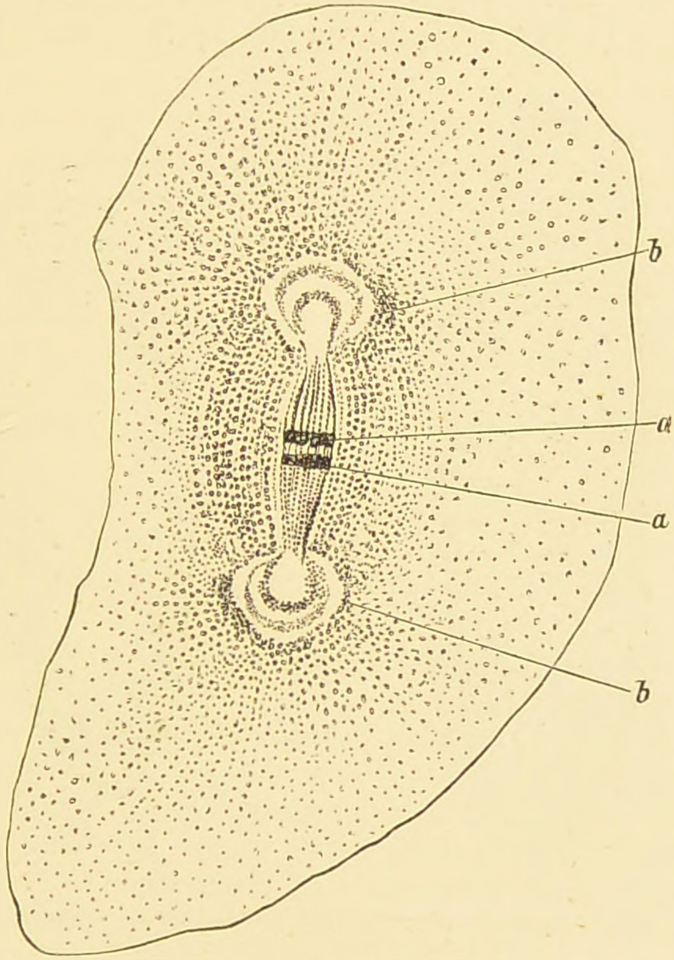
Among invertebrates, brood-chambers or cradles for the young are not uncommon. The capsules of hydroids, the tent of spines on a few sea-urchins, the depressions in the skin in one or two sea-cucumbers, the modified tentacles of some marine annelids, the dorsal shell-chamber in water-fleas, the incurved abdomen of higher crustaceans, the gill-cavities of bivalves, the beautiful brood-shell of the argonaut, illustrate a habit even an outline of which is beyond our limits.

§ 10. *Nemesis of Reproduction.*—We have already shown how reproduction in its origin is linked to death. The primitive ruptures by which the protozoon reduces encumbering bulk, saves its own life, and multiplies its kind, are only a step or two from more diffuse dissolution which is death.

The association of death and reproduction is indeed patent enough, but the connection is in popular language usually misstated. Organisms, one hears, have to die; they must therefore reproduce, else the species would come to an end. But such emphasis on posterior utilities is almost always only an afterthought of our invention. The statement must be corrected by another; as Goette says, "it is not death that makes reproduction necessary, but reproduction has death as its inevitable consequence." This of course refers primarily to the incipient forms of both these katabolic processes.

It is necessary to give a few illustrations. Goette refers to Haeckel's *Magosphæra*, a protozoon which just as it had formed for itself a multicellular body broke up into the component

units. These lived on, and there was no corpse, but at the same time the multicellular colony was no more. Again he takes the case of the lowly and somewhat enigmatical orthonectids, which Van Beneden has classed as Mesozoa, between the single-celled and the stable many-celled animals. In some of these the mature female forms numerous germ-cells, and terminates her individual life by bursting. The germs are

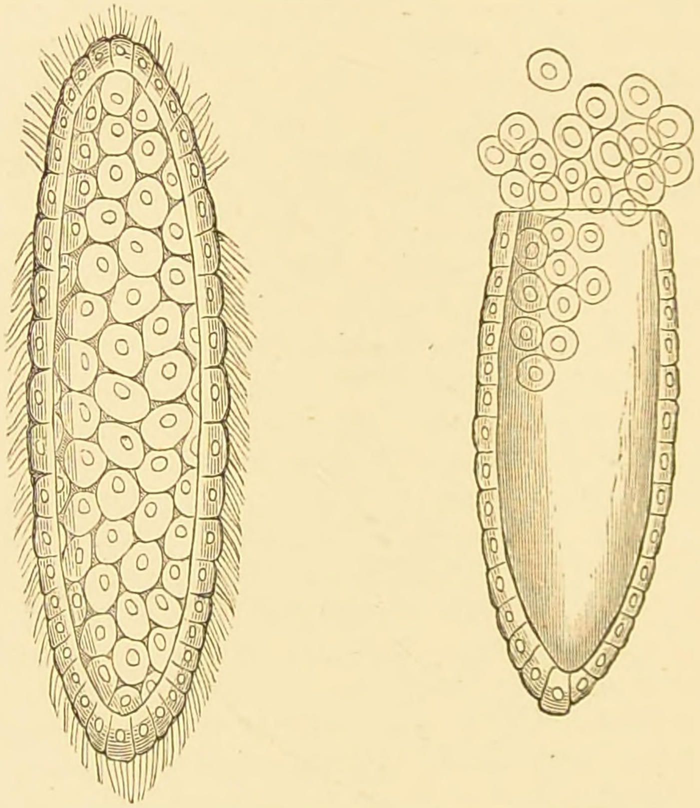


A figure of cell division suggesting the internal disruptions and rearrangements of the nucleus (*a*) and protoplasm.—From Rauber.

liberated, the mother animal has been sacrificed in reproduction. "The death is an altogether inevitable consequence of the reproduction."

Nor is this sacrifice confined to the incipient multicellular organisms. Thus in some species of the annelid *Polygordius*, the mature females break up and die in liberating their ova.

In the "Heteronereis," or sexually modified form of Nereid worms, the whole animal dies after the emission of the genital products. This is approached, but suggestively avoided, in some other Polychaet worms, *e.g.*, the Syllidæ and the *Clitomastus*. The whole organism is not sacrificed, but only a modified portion of the body. This is probably also the case with the famous Palolo-worm (*Eunice viridis*). Here in fact we have one of the keynotes to reproductive differentiation,—the sacrifice is lessened, and the fatality thus warded off.



Orthonectids, showing the rupture of the female in liberating the germs.—From Goette, after Julin.

But again, we find in some threadworms or nematodes (*e.g.*, *Ascaris dactyluris*) that the young live at the expense of the mother, until she is reduced to a mere husk. In fresh-water Polyzoa, Kraepelin notes that the ciliated embryo leaves the maternal body-cavity through a *prolapsus uteri* of the sacrificed mother. In the precocious reproduction of some midge larvæ (*Chironomus*, &c.), the production of young is fatal through successive generations.

Both Weismann and Goette, though with different interpretations, note how many insects (locusts, butterflies, ephemerids, &c.) die a few hours after the production of ova. The exhaustion is fatal, and the males are also involved. In fact, as we should expect from the katabolic temperament, it is the males which are especially liable to exhaustion. The males of some spiders normally die after impregnating the female, a fact perhaps helping to throw light upon the sacrifice of others to their mates. The similarly tiny (ultra-katabolic) male rotifer—an ideal but too unpractical lover, with not even an alimentary canal—would seem usually to fail and expire prematurely, leaving the female to undisturbed parthenogenesis. Every one is familiar with the close association of love and death in the common mayflies. Emergence into winged liberty, the love-dance and the process of fertilisation, the deposition of eggs and the death of both parents, are often the crowded events of a few hours. In higher animals, the fatality of the reproductive sacrifice has been greatly lessened, yet death may tragically persist, even in human life, as the direct nemesis of love.

The temporarily exhausting effect of even moderate sexual indulgence is well known, as well as the increased liability to all forms of disease while the individual energies are thus lowered.

§ 11. *Organic Immortality.*—Comparatively little is yet known about the length of life among lower animals, but there is no reason to doubt that all multicellular organisms die. We have just emphasised the view of Goette, and other naturalists, that reproduction is the beginning of death; which is not inconsistent with the apparent paradox, that local death was the beginning of reproduction. Allowing, then, that multicellular organisms at any rate are mortal, and that the very blossoming of the life in reproduction is fated with a prophecy of death which is its own fulfilment, we have to face two questions,—What of death in the Protozoa? and, In what sense is there an immortality throughout the organic series?

Often enough already, in the preceding pages, we have had to reiterate the contrasts between the Protozoa and the higher animals. These firstlings are single cells physiologically complete in themselves, and have at least very great, if not unlimited, powers of self-recuperation. They leave off where higher animal life begins, that is to say, in a unicellular state.

They do not form "bodies." Their reproduction, moreover, is in the majority simple cell-division into two. If there be loss of individuality, there is hardly loss of life. Death is not so serious when there is nothing left to bury. Nor in most cases can one half of the divided unit be the mother individual, and the other the daughter, for the two appear indistinguishably the same. Thus an idea, broached long ago by Ehrenberg, has been revived and elaborated by several naturalists, and especially by Weismann, that the Protozoa are virtually immortal.

In Weismann's own words, "Natural death occurs only among multicellular organisms, the single-celled forms escape it. There is no end to their development which can be likened to death, nor is the rise of new individuals associated with the death of the old. In the division the two portions are equal, neither is the older nor the younger. Thus there arises an unending series of individuals, each as old as the species itself, each with the power of living on indefinitely, ever dividing but never dying." Ray Lankester puts the matter tersely, "It results from the constitution of the protozoon body as a single cell, and its method of multiplication by fission, that death has no place as a natural recurrent phenomenon among these organisms."

Some limitations must be noticed, which make this idea of pristine immortality yet more emphatic. It is only asserted that the Protozoa escape "natural death," a violent fate may of course await them like any other organisms. They have no charmed life, being as liable to be devoured as those of higher degree. In relation to the environment, however, their simplicity gives them a peculiar power of avoiding impending destiny. The habit of forming protective cysts is very general, and thus enwrapped they can, like the ova and a few of the adults of some higher animals, endure even prolonged desiccation with successful patience, which is rewarded by a rejuvenescence when the rain revisits the pools. But the doctrine of the "immortality of the Protozoa" refers to a defiance of natural, not violent, death.

The psychological objection that the original individuality is extinguished when it divides into two, intrudes a conception which is hardly applicable. The individualities are doubled, nothing is really lost. Most seriously difficult are those cases where the protozoon produces a series of buds,

spores, or division units, and leaves a residual core or unused remnant behind to die. But in regard to the gregarines, for instance, where such a remnant is often left, it has been fairly answered that the residue is rather a kind of excretion than the parent left to perish after its reproductive sacrifice. Weismann is, however, willing to admit the possibility, that in the suctorial Acinetæ, and in the parasitic gregarines, which are both somewhat removed from the normal protozoon type, there may be cases of true mortality.

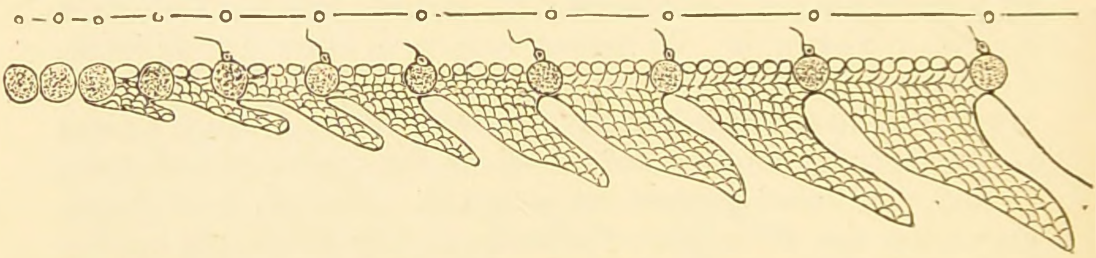
Another point in regard to which experts differ, is whether the Protozoa are really quite self-recuperative. They suffer injuries, they necessarily suffer waste, portions are used up and ejected. The question then arises, Are those acquired defects obliterated, or do they become intensified? Is the wasting only a local death, or is it the beginning of a true senescence? This is a question which can only be answered by observation; *a priori* reasoning is here futile. The most serious criticism of Weismann's view is due to Maupas. Already we have noted his important result, that conjugation is essential to the health of the species. Without this incipient sexual reproduction, the individuals in the course of numerous successive asexual generations grow old. The nucleus degenerates, the size diminishes, the entire energy wanes, the senility ends in death. Maupas believes that all organisms are fated to suffer decay and death, and protests strongly against Weismann's theory that death began with the Metazoa.

It must be noted, however, that in natural conditions the conjugation, prohibited in Maupas's experiments, occurs when it is wanted, and the life flows on. Furthermore, in many Protozoa conjugation has not been shown to occur. It seems therefore more warrantable to insert Maupas's result as a saving clause to Weismann's doctrine, than to regard it as contradictory. The conclusion at present justifiable, is that Protozoa not too highly differentiated, living in natural conditions where conjugation is possible, have a freedom from natural death. To this must then be added the demonstrated saving clause, that in ciliated infusorians, conjugation, which here means an exchange of nuclear elements, is the necessary condition of eternal youth and immortality.

Accepting then, with an emphasised proviso, the general conclusion that most, if not all, unicellular organisms enjoy immortality, that in being without the bondage of a "body"

they are necessarily freed from death, we pass to consider the second question, What does the death of the higher and multicellular organisms really involve?

If death do not naturally occur in the Protozoa, it is evident that it cannot be an inherent characteristic of living matter. Yet it is universal among the multicellular animals. Death, we may thus say, is the price paid for a body, the penalty its attainment and possession sooner or later involves. Now, by a body is meant a complex colony of cells, in which there is more or less division of labour, where the component units are no longer, like the Protozoa, in possession of all their faculties, but through division of labour have only restricted functions and limited powers of self-recuperation. Like Maupas's isolated family of infusorians, the cells of the body do not conjugate with one another; and though they divide and re-divide for a season, the life eventually runs itself out.



The relation between reproductive cells and the body. The horizontal chain of cells represents a succession of the ova from which the "bodies" are produced. At each generation, a spermatozoon fertilising the liberated ovum is also indicated.

A moment's consideration, however, will show that in most cases the organism does not wholly die. Some of the cells usually escape from the bondage of the body as reproductive elements,—as, in fact, Protozoa once more. The majority of these may indeed be lost; eggs which do not meet with male elements perish, and the latter have even less power of independent vitality. But when the ova are fertilised, and proceed to develop into other individuals, it is plain that the parent organisms have not wholly died, since two of their cells have united to start afresh as new plants or animals. In other words, what is new in the multicellular organism, namely, the "body," does indeed die, but the reproductive elements, which correspond to the Protozoa, live on.

This may be made more definite in the preceding diagram. There it is seen that the organism starts like a protozoon, as a single cell, or usually as a union of two cells in the fertilised

ovum. This divides, and its daughter-cells divide and re-divide. They arrange themselves in layers, and are gradually mapped out into the various tissues or organs. In division of labour, they become restricted in their functions, and specialised in their structure. They become differentiated as muscle-cells, nerve-cells, gland-cells, and so on. The result is a more or less complex "body," unstable in its equilibrium because of its very complexity, composed moreover of competing cells far removed from the protozoan all-roundness of function, limited in their powers of recuperation, and emphatically liable to local and periodic, or to general and final death. But the body is not all. At an early stage in some cases, sooner or later always, reproductive cells are set apart. These remain simple and undifferentiated, preserving the structural and functional traditions of the original germ-cell. These cells, and the results of their division, are but little implicated in the differentiation which makes the multicellular organism what it is; they remain simple primitive cells like the Protozoa, and in a sense they too share the protozoon immortality. The diagram shows how one of these cells, separated from the parent organism (and uniting in most cases with a germ-cell of different origin), becomes the beginning of a new body, and, at the same time, necessarily the origin of a new chain, or rather of a continued chain of fresh reproductive cells.

"The body or *soma*," Weismann says, "thus appears to a certain extent as a subsidiary appendage of the true bearers of the life,—the reproductive cells." Ray Lankester has again well expressed this:—"Among the multicellular animals, certain cells are separated from the rest of the constituent units of the body, as egg-cells and sperm-cells; these conjugate and continue to live, whilst the remaining cells, the mere carriers as it were of the immortal reproductive cells, die and disintegrate. The bodies of the higher animals which die, may from this point of view be regarded as something temporary and non-essential, destined merely to carry for a time, to nurse, and to nourish the more important and deathless fission-products of the unicellular egg."

In most cases, as Weismann insists, it is more correct to speak of "the continuity of the germinal protoplasm" than of the continuity of the germ-cells; but, with this proviso, the diagram expresses a fact most important in understanding reproduction and heredity, that the chain of life is in a real

sense continuous, and that the "bodies" which die are deciduous growths, which arise round about the real links. The bodies are but the torches which burn out, while the living flame has passed throughout the organic series unextinguished. The bodies are the leaves which fall in dying from the continuously growing branch. Thus although death take inexorable grasp of the individual, the continuance of the life is still in a deep sense unaffected; the reproductive elements have already claimed their protozoan immortality, are already recreating a new body; so in the simplest physical, as in the highest psychic life, we may say that love is stronger than death.

SUMMARY.

1. According to Weismann's theory of the continuity of the germ-plasm, a portion of the specific hereditary substance which the fertilised ovum contains is not used up in the development of the offspring's body, but is reserved unchanged to form the germ-cells of the following generation.

2. Sexual maturity generally occurs towards the limit of growth, is marked by liberation of reproductive elements and by secondary characteristics, in part due to the reaction of the reproductive function on the general system. Precocious maturity may be due to constitutional or environmental conditions, and has been of much importance in the evolution of flowering plants.

3. Menstruation may be interpreted as a means of getting rid of the anabolic surplus of the female in absence of its fœtal consumption.

4. Sexual union, at first very passive and random, becomes active and definite with the gradual evolution of sex and secondary sexual organs.

5. Birth is at first accomplished by rupture, but becomes a definite process usually effected through special ducts. Oviparous and viviparous birth only differ in degree.

6. Early nutrition is usually an absorption of the yolk, but in mammals is accomplished by osmotic transfusion from the blood of the mother to that of the fœtus.

7. Lactation may be interpreted as an anabolic overflow.

8. Besides milk, there are other secretions associated with the nutrition and sheltering of the young. Pigeon's milk, edible birds' nests, and the mucous threads of sticklebacks, are illustrations.

9. Incubation, reaching a climax in birds, is paralleled in many other classes.

10. Reproduction and death both represent katabolic crises. Primitively, they are nearly akin. Reproduction may ward off death from the Protozoon, but in the simplest Metazoa it helped to cause it.

11. The Protozoa come nearer immortality than other organisms. The fact of germinal continuity involves an organic immortality.

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CHAPTER XIX.

Psychological and Ethical Aspects.

§ 1. *Common Ground between Animals and Men.*—Hitherto we have been justifying the orthodoxy of an anatomical training, by almost wholly ignoring the fact that animals have a psychic life, or only mentioning the mere neural aspect of functions. Only in discussing sexual selection, and the general facts of sexual union and of parentage, have we intruded words like "care," "sacrifice," and "love." A purely physiological treatment of sex and reproduction is, however, obviously incomplete. It would be rejected with scorn in reference to human life; it must be equally rejected in regard to the higher animals, which, taken together, exhibit the analogues of almost every human emotion, and of all our less recondite intellectual processes. It is with emotions that we have here most to do; and without raising the difficult question whether animals exhibit any emotions exactly analogous to those which in man are associated with the "moral sense," "religion," and "the sublime," we accept the conclusion of Darwin, followed by Romanes and others, that all other emotions which we ourselves experience, are likewise recognisable in *analogous* expression in the higher animals. Those which are associated with sex and reproduction are indeed among the most patent; love of mates, love of offspring, lust, jealousy, family affection, social sympathies, are undeniable.

§ 2. *The Love of Mates.*—In the lowest animals, where two exhausted cells flow together in incipient sexual union, there is apparently only one component of that most complex musical chord in life which we call "love." There is physical attraction, and the whole process is very much a satisfaction of protoplasmic hunger.

In multicellular animals, the liberation of sex-elements is at first very passive. It concerns the individual alone. Fertilisation is a random matter; and though sex exists, sexual attraction does not.

A grade higher, true sexual union begins to appear. But at first this simply occurs between any male and any available female. The psychological factor is still but feebly expressed; there is no genuine pairing, and it would be folly to use the word love in such cases.

Gradually, however, for instance among insects, the sexes associate in pairs. There is some psychic sexual attraction, often accompanied with no little courtship, but much more important is the occasional maintenance of the association for a lengthened period. There may even be co-operation in work, as in dung-rolling beetles such as *Ateuchus*, where the two sexes pursue their somewhat disinterested labours together. The male and female of another lamellicorn beetle (*Lethrus cephalotes*) inhabit the same cavity, and the virtuous matron is said greatly to resent the intrusion of another male. As degenerate offshoots from the path of psychic progress, or as illustrations of the predominance of merely physical attraction, one must regard such prolonged associations of the two sexes as are seen in the formidable parasitic worm *Bilharzia*, where the male carries the female about, or in some parasitic crustaceans where the positions are reversed.

Among the cold-blooded fishes, the battles of the stickleback with his rivals, his captivating manœuvres to lead the female to the nest which he has built, his mad dance of passion around her, and his subsequent jealous guarding of the nest, have often been observed and admired. In one of the sunfishes the male and female alternate in guarding the ova. The monogamous habits of the salmon, and the frequently fatal contests between rival males are well known. Carbonnier has beautifully described the elaborateness of sexual display and the ardency of passion in the male butterfly-fish, and also in the rainbow-fish of the Ganges.

The amatory croaking of frogs, the love-gambols of some newts, the curious parental care of some male amphibians mentioned in the preceding chapter, and the like, illustrate the continuance of more than crude physical attraction between the sexes. Of many amphibians it may be said that it is only in their sexual and reproductive relations that they seem to wake up out of their constitutional sluggishness.

In regard to reptiles, little is known beyond the exhibition of sexual passion and the jealous combats of rival males. Yet Romanes refers to the interesting fact that when a cobra is

killed, its mate is often found on the same spot a day or two afterwards.

Among birds and mammals, the greater differentiation of the nervous system and the higher pitch of the whole life is associated with the development of what pedantry alone can refuse to call love. There is often partnership, co-operation, and evident affection beyond the limits of the breeding periods, there are abundant illustrations of regard for conventions, there are close analogues of human flirtation, courtship, jealousy, and even crime, though, so far as we understand the matter, there is no convincing evidence of what may be called a distinctively moral judgment. There is no doubt that in the two highest classes of animals at least, the physical sympathies of sexuality have been enhanced by the emotional, if not also intellectual, sympathies of love. Those sceptical on this point should consult such a work as Büchner's "Liebe und Liebesleben in der Thierwelt," or Sutherland's "Origin and Growth of the Moral Instinct" (1898), which contain an overflowing wealth of instances.

§ 3. *Sexual Attraction.*—Mantegazza has written a work entitled "The Physiology of Love," in which he expounds the optimistic doctrine that love is the universal dynamic; and from this Büchner quotes the sentence, that "the whole of nature is one hymn of love." If the last word be used very widely, this often-repeated utterance has more than poetic significance. But even in the most literal sense there is much truth in it, since so many animals are at one in the common habit of serenading their mates. The chirping of insects, the croaking of frogs, the calls of mammals, the song of birds, illustrate both the bathos and glory of the love-chorus. The works of Darwin and others have made us familiar with the numerous ways, both gentle and violent, in which mammals woo one another. The display of decorations in which many male birds indulge, the amatory dances of others, the love-lights of glow-insects, the joyous tournaments or furious duels of rival suitors, the choice which not a few females seem to exhibit, and the like, show how a process, at first crude enough, becomes enhanced by appeals to more than merely sexual appetite. But it is hardly necessary now to argue seriously in support of the thesis that love—in the sense of sexual sympathy, psychical as well as physical—exists among animals in many degrees of evolution. Our comparative

psychology has been too much influenced by our intellectual superiority; but while this, no doubt, has its correspondingly increased possibilities of emotional range, it does not necessarily imply a corresponding emotional intensity; and we have no means of measuring, much less limiting, that glow of organic emotion which so manifestly flushes the organism with colour and floods the world with song. Who knows whether the song-bird be not beside the man what the child-musician is to the ordinary dulness of our daily toil and thought? The fact to be insisted upon is this, that the vague sexual attraction of the lowest organisms has been evolved into a definite reproductive impulse, into a desire often predominating over even that of self-preservation; that this again, enhanced by more and more subtle psychical additions, passes by a gentle gradient into the love of the highest animals, and of the average human individual.

But the possibilities of evolution are not ended, and though some may shrink from that comparison of human love with its analogues in the organic series, the theory of evolution offers the precise compensation such natures require. Without recognising the possibilities of individual and of racial evolution, we are shut up to the conventional view that the poet and his heroine alike are exceptional creations, hopelessly beyond the everyday average of the race. Whereas, admitting the idea of evolution, we are not only entitled to the hope, but logically compelled to the assurance, that these rare fruits of an apparently more than earthly paradise of love, which only the forerunners of the race have been privileged to gather, or it may be to see from distant heights, are yet the realities of a daily life towards which we and ours may journey.

§ 4. *Intellectual and Emotional Differences between the Sexes.*—We have seen that a deep difference in constitution expresses itself in the distinctions between male and female, whether these be physical or mental. The differences may be exaggerated or lessened, but to obliterate them it would be necessary to have all the evolution over again on a new basis. What was decided among the prehistoric Protozoa cannot be annulled by Act of Parliament. In this mere outline we cannot of course do more than indicate the relation of the biological differences between the sexes to the resulting psychological and social differentiations; for more than this neither space nor powers suffice. We must insist upon the

biological considerations underlying the relation of the sexes, which have been too much discussed by contemporary writers of all schools as if the known facts of sex did not exist at all, or almost if these were a mere matter of muscular strength or weight of brain.

The reader need not be reminded of the oldest and most traditional views of the subjection of women inherited from the ancient European order; still less perhaps of the attitude of the ordinary politician, who supposes that the matter is one essentially to be settled by the giving or withholding of the franchise. The exclusively political view of the problem has in turn been to a large extent subordinated to that of economic *laissez-faire*, from which of course it consistently appeared that all things would be settled as soon as women were sufficiently plunged into the competitive industrial struggle for their own daily bread. While, as the complexly ruinous results of this inter-sexual competition for subsistence upon both sexes and upon family life have begun to become manifest, the more recent economic panacea of redistribution of wealth has naturally been invoked, and we have merely somehow to raise women's wages.

All disputants have tolerably agreed in neglecting the historic, and still more the biological factors; while, so far as the past evolution of the present state of things is taken into account at all, the position of women is regarded as having simply been that in which the stronger muscle and brain of man was able to place her. The past of the race is thus depicted in the most sinister colours, and the whole view is supposed to be confirmed by appeal to the practice of the most degenerate races, and this again as described with the scanty sympathy or impartiality of the average white traveller, missionary, or settler.

As we have already said, we cannot attempt a full discussion of the question, but our book would be left without point, and its essential thesis useless, if we did not, in conclusion, seek to call attention to the fundamental facts of organic difference, say rather divergent lines of differentiation, underlying the whole problem of the sexes. We shall only suggest, as the best argument for the adoption of our standpoint, the way in which it becomes possible relatively to harmonise the very diverse outlooks. We shall not so readily abuse the poor savage, who lies idle in the sun for days after

his return from the hunting, while his heavy-laden wife toils and moils without complaint or cease; but bearing in view the extreme bursts of exertion which such a life of incessant struggle with nature and his fellows for food and for life involves upon him, and the consequent necessity of correspondingly utilising every opportunity of repose to recruit and eke out the short and precarious life so indispensable to wife and weans, we shall see that this crude domestic economy is the best, the most moral, and the most kindly attainable under the circumstances. Again, the traveller from town, who thinks the agricultural labourer a greedy brute for eating the morsel of bacon and leaving his wife and children only the bread, does not see that by acting otherwise the total ration would soon be still further lowered, by diminished earnings, loss of employment, or loss of health.

The actual relations of fisherman and fishwife, of the smallest farmer and his wife, seem to us to give a truer as well as a healthier picture of antique industrial society, than those we find in current literature; and if we admit that such life is deficient in refinement (although, on all deeper grounds, from religion to ballad poetry, we might even largely dispute this), it has still much to teach in respect of simplicity and health.

The old view of the subjection of women was not, in fact, so much of tyranny as it seemed, but roughly tended to express the average division of labour; of course hardships were frequent, but these have been exaggerated. The absolute ratification of this by law and religion was merely of a piece with the whole order of belief and practice, in which men crushed themselves still more than their mates. Being absolute, however, such theories had to be overthrown, and the application of the idea of equality, which had done such good service in demolishing the established castes, was a natural and serviceable one. We have above traced the development of this, however, and it is now full time to re-emphasise, this time of course with all scientific relativity instead of a dogmatic authority, the biological factors of the case, and to suggest their possible service in destroying the economic fallacies at present so prevalent, and still more towards reconstituting that complex and sympathetic co-operation between the differentiated sexes in and around which all progress past or future must depend. Instead of men and women merely labouring

to produce things as the past economic theories insisted, or competing over the distribution of them, as we at present think so important, a further swing of economic theory will lead us round upon a higher spiral to the direct organic facts. So it is not for the sake of production or distribution, of self-interest or mechanism, or any other idol of the economists, that the male organism organises the climax of his life's struggle and labour, but for his mate; as she, and then he, also for their little ones. Production is for consumption; the species is its own highest, its sole essential product. The social order will clear itself, as it comes more in touch with biology.

It is equally certain that the two sexes are complementary and mutually dependent. Virtually asexual organisms, like Bacteria, occupy no high place in Nature's roll of honour; virtually unisexual organisms, like many rotifers, are great rarities. Parthenogenesis may be an organic ideal, but it is one which has been rarely realised. Males and females, like the sex-elements, are mutually dependent, and that not merely because they are males and females, but also in functions not directly associated with those of sex. To dispute whether males or females are the higher, is like disputing the relative superiority of animals and plants. Each is higher in its own way, and the two are complementary.

While there are broad general distinctions between the intellectual, and especially the emotional, characteristics of males and females among the higher animals, these not unfrequently tend to become mingled. There is, however, no evidence that they might be gradually obliterated. The males of the sea-horse, the obstetric frog, and many birds discharge maternal functions, and there are females who fight for the males, and are stronger, or more passionate than their mates. But these are rarities. It is generally true that the males are more active, energetic, eager, passionate, and variable; the females more passive, conservative, sluggish, and stable. The males, or, to return to the terms of our thesis, the more katabolic organisms, often seem more variable, and therefore, as Brooks has emphasised, may have frequently been the leaders in evolutionary progress, while the more anabolic females tend rather to preserve the constancy and integrity of the species.

There are some cases, as illustrated notably by the contrast between ruffs and reeves, where the greater variability of the

males along certain lines seems obvious, but, according to Karl Pearson, the doctrine that man is more variable than woman is a pseudo-scientific superstition, based on inadequate or inadmissible data. The examination of seventeen groups of measurements of different parts of the body shows that in eleven groups the female is more variable than the male, and in six the male more than the female. The differences of variability, however, are slight, less than those between members of the same race living in different conditions; they are perhaps due to differences in the severity of the struggle for existence. (See "The Chances of Death, and other Studies in Evolution," 2 vols., London, 1897, pp. 388 and 460.)

Along paths where the reproductive sacrifice was one of the determinants of progress, the females must have the credit of leading the way. The more active males, with a consequently wider range of experience, may have bigger brains and more intelligence; but the females, especially as mothers, have indubitably a larger and more habitual share of the altruistic emotions. The males being usually stronger, have greater independence and courage; the females excel in constancy of affection and in sympathy. The spasmodic bursts of activity characteristic of males contrast with the continuous patience of the females, which we take to be an expression of constitutional contrast, and by no means, as some would have us believe, a mere product of masculine bullying. The stronger lust and passion of males is likewise the obverse of predominant katabolism.

That men should have greater cerebral variability and therefore more originality, while women have greater stability and therefore more "common sense," are facts both consistent with the general theory of sex and verifiable in common experience. The woman, conserving the effects of past variations, has what may be called the greater integrating intelligence; the man, introducing new variations, is stronger in differentiation. The feminine passivity is expressed in greater patience, more open-mindedness, greater appreciation of subtle details, and consequently what we call more rapid intuition. The masculine activity lends a greater power of maximum effort, of scientific insight, or cerebral experiment with impressions, and is associated with an unobservant or impatient disregard of minute details, but with a stronger grasp of

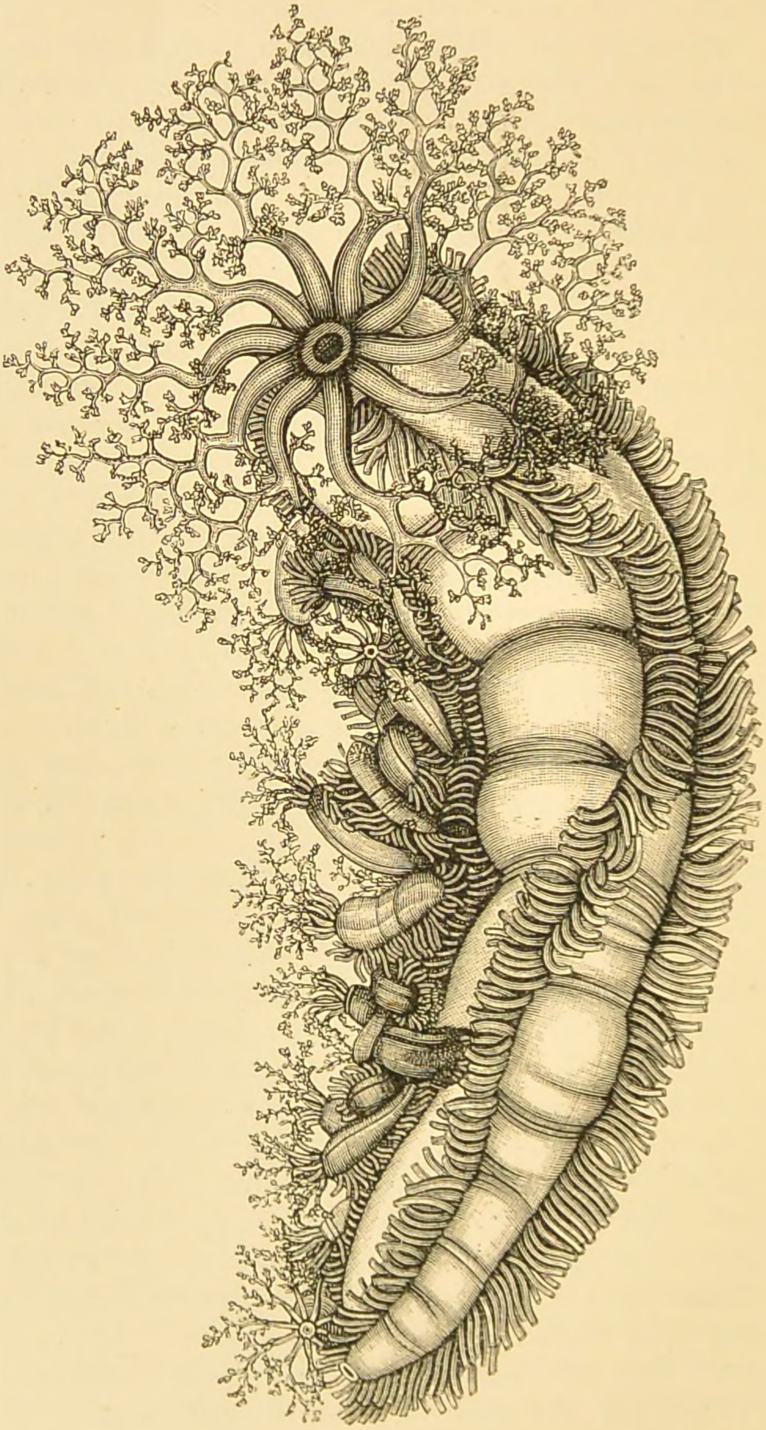
generalities. Man thinks more, women feels more. He discovers more, but remembers less; she is more receptive, and less forgetful.

§ 5. *The Love for Offspring.*—Just as it is impossible to point to the stage where psychical sympathies enhance the reproductive impulse into the love of mates, so we cannot tell where parental care becomes disinterested enough to warrant our calling it love of offspring. For, as no one can be foolish enough deliberately to ignore the sexual or physical basis of "love" in the higher and highest organisms, so it must be allowed that even maternal care has its selfish side. To take only one example, that of lactation. The unrelieved pressure in the mammary glands of a mother animal robbed of her young is no doubt largely concerned in prompting her to adopt young ones not her own, yet we soon see these established in her affections. So in normal cases, there naturally remains an alloy which prevents us from regarding even maternal care as altogether disinterested. In all such cases, our interpretations risk an undue materialism on the one hand, and an undue transcendentalism on the other; and while our modern temper may habitually incline us to the former, we must not be too fond of taking for granted that all the common-sense is on that side, for we must remember that the course of evolution not only has been, but must be, towards the other.

Among animals low down in the organic series there is often a close association between mother and offspring. Even in some cœlenterates and worms the offspring cling about the mother animals, and may be protected in various kinds of brood-chambers. The little freshwater leech, *Clepsine*, carries its young about with it, fixed to its ventral surface. A marine leech, known as the skate-sucker (*Pontobdella muricata*), mounts guard for weeks over the eggs which are laid in a bivalve shell or the like. It is probable that this habit has protective value, but whether from active enemies or from accumulations of sand and mud is uncertain. In an aquarium one of these leeches continued to incubate for one hundred and twenty-three days.

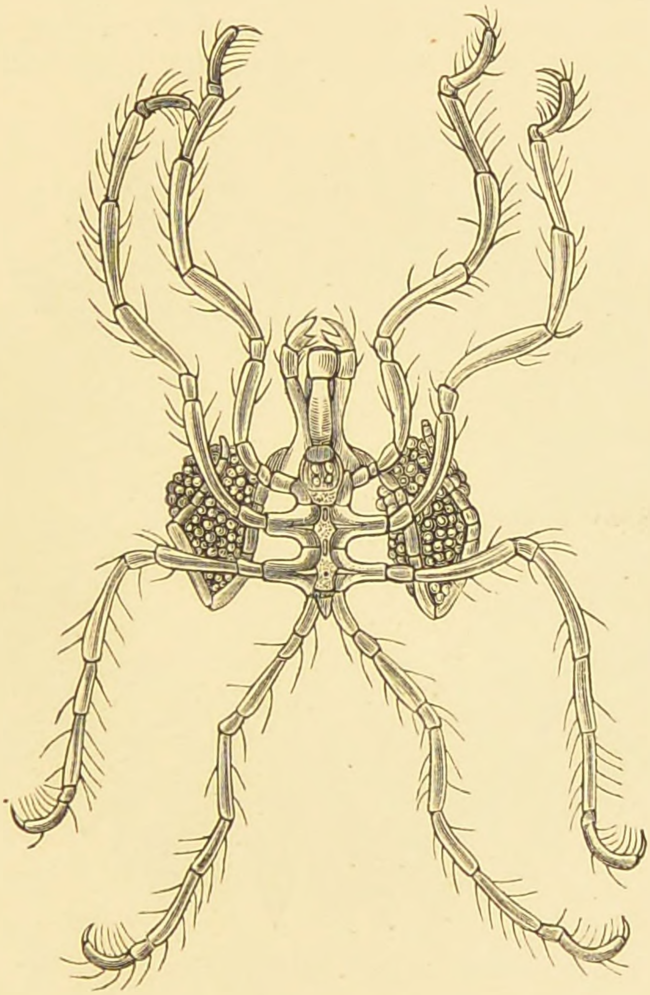
In some sea-urchins and starfishes there are simple forms of brood-care, but the case of Holothurians is perhaps more interesting. Prolonged attachment between the young ones and the mother is known in at least nine species, of which five

are antarctic and one arctic. The mode of attachment differs markedly in different forms, thus each of the five antarctic



A Sea-cucumber, or Holothurian (*Cucumaria crocea*), with numerous young attached to the skin.—From Carus Sterne, after "Challenger" Narrative.

species has its young attached in a different way. In *Psolus ephippifer* the young develop among the dorsal plates; in *Psolus antarcticus*, on the ventral surface; in *Cucumaria crocea*, on the modified dorsal ambulacra; in *Cucumaria lævigata*, in ventral pouches; and in *Chirodota contorta*, in the genital tubes. (See H. Ludwig, "Zool. Anzeiger," xx., 1897, pp. 217-219.) The

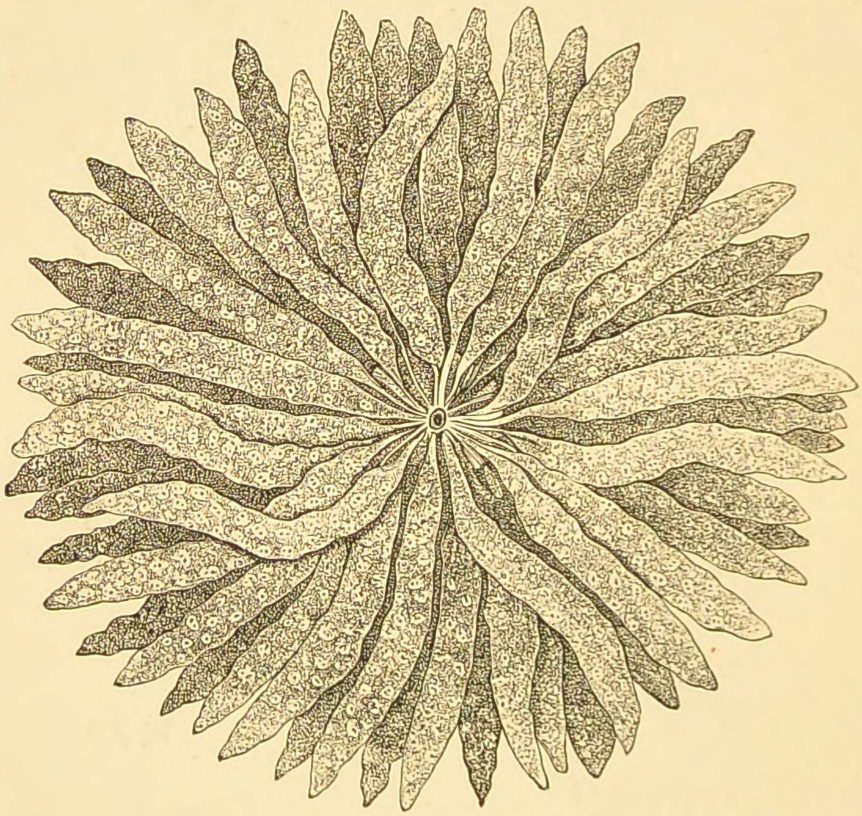


A Male "Sea-spider," or Pycnogonid, carrying the ova.—
After Carus Sterne.

interpretation here evidently does not lie with the morphologist; is he not compelled to speculate on the beginnings of psychic life in the strangely rudimental nervous system of these forms from which even definite ganglia seem absent? Yet even here we have motherhood protecting offspring, perhaps all the more because of the prevailing cold; perhaps

of course also as a protection from premature burial in soft muddy bottoms.

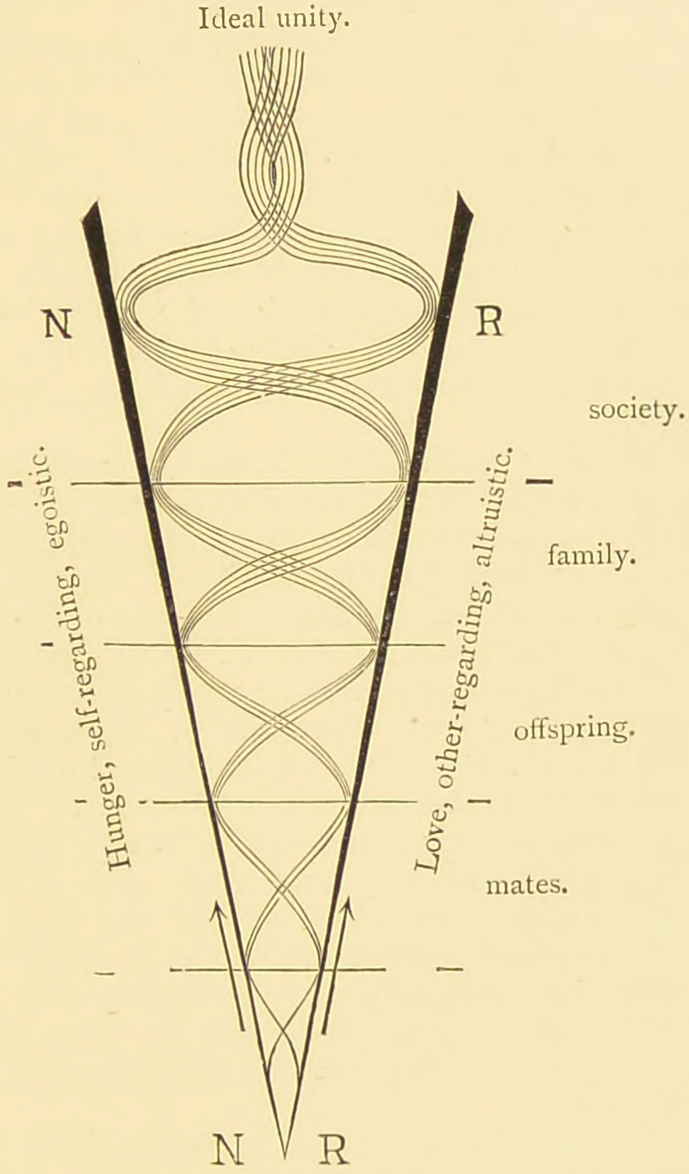
In some lowly crustaceans, the young may return to the shell-cavity of the mother after hatching, and even after they have undergone a moult. The young crayfish are said to return to the maternal shelter after they have been set adrift. The care of the nurse-bees for their charge, though not exactly maternal, deserves to be recalled; and the way in which ants save the cocoons when danger threatens is well known. De



Egg-Clusters of a species of Cuttlefish.—From Von Hayek.

Geer describes how one of the insects infesting plants behaves to her young brood exactly like a hen with her chickens; and Bonnet vividly describes a case where a mother spider, at the mercy of an ant-lion, fought for her eggs at the sacrifice of her own life. Some spiders, too, carry their young; and some crustaceans swim along with their young ones. Some cuttlefishes are careful in keeping their egg clusters clean and safe; while even the headless fresh-water mussel retains her young,

when there is no fish present to which they may attach themselves. In fishes, it must be allowed that the care, if at all evident, is usually paternal; in amphibians, it is rare; in



Diagrammatic Representation of the Relations between Nutritive, Self-Maintaining, or Egoistic, and Reproductive, Species-Regarding, or Altruistic Activities.

reptiles, somewhat more marked. In birds and mammals, however, parental care is general, and unquestionably grows into love for offspring.

§ 6. *Egoism and Altruism.*—The optimism which finds in

animal life only "one hymn of love" is inaccurate, like the pessimism which sees throughout nothing but selfishness. Littré, Leconte, and some others less definitely, have more reasonably recognised the co-existence of twin streams of egoism and altruism, which often merge for a space without losing their distinctness, and are traceable to a common origin in the simplest forms of life. In the hunger and reproductive attractions of the lowest organisms, the self-regarding and other-regarding activities of the higher find their starting-point. Though some vague consciousness is perhaps co-existent with life itself, we can only speak with confidence of psychical egoism and altruism after a central nervous system has been definitely established. At the same time, the activities of even the lowest organisms are often distinctly referable to either category.

A simple organism, which merely feeds and grows, and liberates superfluous portions of its substance to start new existences, is plainly living an egoistic and individualistic life. But whenever we find the occurrence of close association with another form, we find the first rude hints of love. It may still be almost wholly an organic hunger which prompts the union, but it is the beginning of life not wholly individualistic. Hardly distinguishable at the outset, the primitive hunger and love become the starting-points of divergent lines of egoistic and altruistic emotion and activity.

The differentiation of separate sexes; the production of offspring which remain associated with the parents; the occurrence of genuine pairing beyond the limits of the sexual period; the establishment of distinct families, with unmistakable affection between parents, offspring, and relatives; and lastly, the occurrence of animal societies wider than the family,—mark important steps in the evolution of both egoism and altruism.

The diagram sums up the important facts. There are two divergent lines of emotional and practical activity,—hunger, self-regarding, egoism, on the one hand; love, other-regarding, altruism, on the other. These find a basal unity in the primitively close association between hunger and love, between nutritive and reproductive needs. Each plane of ascent marks a widening and ennobling of the activities; but each has its corresponding bathos, when either side unduly preponderates over the other. The actual path of progress is represented by

action and reaction between the two complementary functions, the mingling becoming more and more intricate. Sexual attraction ceases to be wholly selfish; hunger may be overcome by love; love of mates is enhanced by love for offspring; love for offspring broadens out into love of kindred. Finally, the ideal before us is a more harmonious blending of the two streams.

SUMMARY.

1. In most of the emotions, and in the simpler intellectual processes, there is common ground between animals and men. This is especially true of the emotions associated with sex and reproduction.

2. The love of mates has its roots in physical sexual attraction, but has been gradually enhanced by psychical sympathies.

3. The modes of sexual attraction rise from the crude and physical to the subtle and psychical.

4. The intellectual and emotional differences between the sexes are correlated with the deep-seated constitutional differences. Males and females are complementary, each higher in its own way.

5. The love for offspring has grown as gradually as the love for mates. Even lactation and maternal care may be in part egoistic. Apart from exceptional cases, genuine love for offspring is only emphatic in birds and mammals, where the reproductive sacrifice of the mother has also been increased.

6. Egoism and altruism have their roots in the primary hunger and love, or nutritive and reproductive activities. The divergent streams of emotion and activity have a common origin, subtly mingle at various turning-points, and ought to blend more and more in one.

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CHAPTER XX.

Laws of Multiplication.

§ 1. *Rate of Reproduction and Rate of Increase.*—We know much more about the rate at which organisms reproduce, than about the rate at which the number of adults in reality increases or decreases. The one fact may be ascertained by observation; the other involves comparative statistics, which are difficult enough to obtain, even for the human species. The rate of reproduction depends upon the constitution of the individual and its immediate environment, including, above all, its nutrition. The rate of increase or decrease depends upon the wide and complex conditions of the entire animate and inanimate environment, or upon the degree of success in the struggle for existence.

That there are enormous differences in the rates of reproduction is very evident. Maupas tells us how a single infusorian becomes in a week the ancestor of a progeny only computable in millions,—of numbers which the progeny of a pair of elephants, supposing they all lived their natural term of years, would not attain to in five centuries. Again, Huxley calculates that the progeny of a single parthenogenetic plant-louse—supposed again to live a charmed life—would in a few months literally outweigh the population of China. The geometrical ratio of reproduction, so often emphasised, would indeed have startling results if it involved real, and not merely potential, increase.

That it does sometimes realise itself for short periods or special areas of favourable conditions is well known; for instance, in the periodic plagues of insects, or in the still unmastered rabbit pest of Australia. But in the established fauna and flora of a country, without intruded importations or marked climatic changes, the rise and fall of population is seldom emphatic. The rate of reproduction is only one factor in the

numerical strength of the species or in its increase. The common tapeworm produces myriads of embryos, but these have only one chance in eighty-five millions (it is said) of succeeding. Many common and numerous animals reproduce very slowly. That some species are on the increase, *e.g.*, bacteria, under the unprecedentedly favourable conditions which our recent "industrial progress" affords, while other species are on the decrease, *e.g.*, many birds, is certain; but the rate of reproduction is not a direct condition in either case.

§ 2. *History of Discussion on Rate of Reproduction.*—In this, as in not a few other cases, the biologist is profoundly indebted to the student of social questions, for no adequate attention was paid to the laws of multiplication before the appearance of the epoch-making "theory of population" of Malthus, nor is it yet possible or profitable to isolate the human question from the general one. Malthus's fundamental proposition is indeed usually softened from its earliest form—that population tends to increase in geometrical, subsistence only in arithmetical ratio—into the simple statement that population tends to outrun subsistence, but has none the less served as a base of weighty deductions for both the naturalist and the economist. From Darwin's standpoint, the "positive checks" to population (disease, starvation, war, infanticide), and the "prudential" (moral or birth-restricting) checks, come to be viewed as special forms of natural or artificial selection, while the fundamental induction has been extended throughout nature as the essential condition of the struggle for existence. After long dispute, the induction of Malthus gained acceptance, followed by wide deductive use and abuse, among economists. Yet, fundamentally important as the subject thus is to naturalist and economist alike, the former has not as yet effected any thorough investigation of the conditions of multiplication, or even usually incorporated the keen analysis which we owe to Spencer, while the economic theorist or disputant frequently still employs the doctrine even in its pre-Darwinian form. It is thus doubly needful to summarise, as briefly as may be, Spencer's elaborate statement of the laws of multiplication.

§ 3. *Summary of Spencer's Analysis.*—Different species exhibit different degrees of fertility, which have become established in process of evolution like the organisms themselves. To understand this particular adaptation of function to conditions of existence, of organism to environment, we may analyse these into their respective factors. It is evident that in the environment of any species there are many conditions with which its individuals

establish a moving equilibrium, sooner or later overthrown in death. To prevent extinction, the organism meets these environing actions in two distinct ways,—(1) by individual adaptations, active thrusts or passive parries; (2) by the production of new individuals to replace those overthrown,—in other words, by *genesis*. The latter may occur, as we have seen, in varied forms, sexual or asexual, and at various rates, which depend upon age, frequency, fertility, and duration of reproduction, together with amount and nature of parental aid. These actions and reactions of environment and organism admit of another grouping in more familiar terms, into two conflicting sets,—(*a*) the forces destructive of race; (*b*) the forces preservative of race.

Leaving aside cases in which permanent predominance of destructive forces causes extinction, and also, as infinitely improbable, cases of perfectly stationary numbers, the inquiry is:—In races that continue to exist, what laws of numerical variation result from these variable conflicting forces that are respectively destructive or preservative of race? How is the alternate excess of one or other rectified? A self-sustaining balance must exist; the alternate predominance of each force must initiate a compensatory excess of the other; how is this to be explained?

When favourable circumstances cause any species to become unusually numerous, an immediate increase of destructive influences, passive as well as active, takes place; competition becomes keener and enemies more abundant, and conversely. Yet this is not the sole, much less the permanent, means of establishing a balance; nor does it explain either the differences in the rate of fertility and mortality, or the adaptation of one to the other. This minor adjustment in fact implies a major one.

The forces preservative of race were seen above to be two,—power to maintain individual life, and power to generate the species. Now, in a species which survives, given the forces destructive of race as a constant quantity, those preservative of race must be a constant quantity also; and, since the latter are two, the individual plus the reproductive, these must vary inversely, one must decrease as the other increases. To this law every species must conform, or cease to exist. Let us restate this at greater length. A species in which self-preservative life is low, and in which the individuals are accordingly rapidly overthrown in the struggle with the destructive forces, must become extinct, unless the other race-preservative factor be proportionally strengthened,—unless, that is to say, its reproductive power become proportionally great. On the other hand, if both preservative factors be increased, if a species of high self-preservative power were also endowed with powers of multiplication beyond what is needful, such success of fertility, if extreme, would cause sudden extinction of the species by starvation, and if less extreme, and so effecting a permanent increase of the numbers of the species, would next bring about such intenser competition, such increased dangers to individual life, that the great self-preservative power would not be more than sufficient to cope with them.

In short, then, we have reached the *a priori* principle, that in races which continuously survive, in which the destructive forces are balanced by the preservative ones, there must be an inverse proportion between the power to sustain individual life and the power to produce new individuals. But what is the physiological explanation of this adjustment, and how has it arisen in process of evolution? Spencer has elsewhere enlarged upon the proposition, which we have already illustrated, that genesis in all its forms

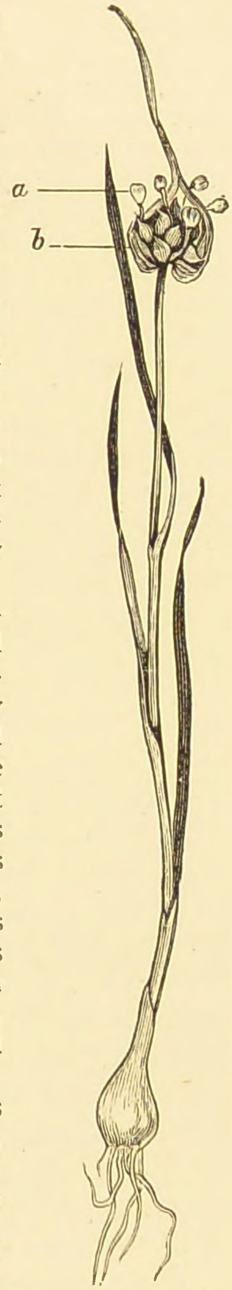
is a process of disintegration, and is thus essentially opposed to that process of integration which is one element of individual evolution. The matter and energy supplied for the young organism represent so much loss for the parent; while, conversely, the larger the amount of matter and energy consumed by the functional actions of the parent, the less must be the amount remaining for those of the offspring. The disintegration which constitutes genesis may be complete or partial, and in the latter case the parent, having reached considerable bulk and complexity before reproduction sets in, may survive the process. In the same way, individual evolution may be expressed in bulk, in structure, in amount or variety of action, or in combinations of these; yet, in any case, this progress of each individuality must correspondingly retard the establishment of the new ones.

While in the first portion of the argument, then, it was shown that a species cannot be maintained unless self-preservative and reproductive power vary inversely, it is now evident that, irrespective of an end to be subserved, these powers cannot do other than vary inversely, and the one *a priori* principle is thus seen to be the obverse of the other. And if we group under the term individuation all those race-preservative processes by which individual life is completed and maintained, and extend the term genesis to include all those processes aiding the formation and perfecting of new individuals, the result of the whole argument may be tersely expressed in the formula,—Individuation and Genesis vary inversely. And from this conception important corollaries open; thus, other things equal, advancing evolution must be accompanied by declining fertility; again, if the difficulties of self-preservation permanently diminish, there will be a permanent increase in the rate of multiplication, and conversely.

In attempting the inductive verification of these *a priori* inferences, practical difficulties arise, owing to the high complexity of each of our two sets of factors and the independent variability of their details, and thus the total cost of individuation and of genesis alike is hard of estimation and comparison. For this purpose, however, there are successively to be investigated,—(1) the antagonism between growth and genesis, sexual and asexual; (2) that between development and genesis; (3) that between expenditure and genesis; and (4) the coincidence between high nutrition and genesis. It is impossible to summarise the wealth of evidence drawn from a wide survey of the animal and vegetable world contained in the chapters devoted to those various heads, but attention may be called to the last and most obscure of these. It is indeed evident *a priori* that, if the cost of individuation be once provided for, a higher nutrition will render possible a greater propagation, sexual or asexual, and this may be abundantly verified by observation and experiment. Witness the case of aphides, in which the rate of parthenogenetic reproduction is found to be directly proportional to temperature and food-supply; or, again, that of domestic animals, such as the sheep, whose fertility is in direct relation to richness of pasture and warmth of climate; or, finally, and most obviously of all, that of field or fruit crops, upon which the influence of increased liberality of manuring will not be disputed. Yet it is sometimes maintained, for both plants and animals, that overfeeding checks increase, while limited nutriment stimulates it; and to support this view there are cited such cases as that of the barrenness of a very luxuriant plant, and the fruitfulness which appears on its depletion. But if this objection really held, manuring would in all cases be inexpedient, instead of only in plants where the growth of sexless axes

is still too luxuriant ; and a tree which has borne a heavy crop should, by this depletion, bear again yet more heavily, instead of being more or less barren next year unless manured. Or the difficulty may also be met by interpreting such vegetative luxuriance, not as a case of higher individuation at all, but simply as a case of asexual multiplication of secondary axes ; or again, and perhaps most simply, by regarding the appearance of sexual reproduction on depletion simply as a case of the previously demonstrated antagonism between genesis and growth.

But again, since fatness is associated with sterility, it is often argued that high feeding is unfavourable to genesis. Obesity, however, is now known to be associated with imperfect assimilation, with physiological impoverishment or degeneration,—by no means with that constitutional wealth which is favourable to fertility. If, in short, we bear in mind that truly high nutrition means only due abundance of, and due proportion among, all the substances which the organism requires, and that their perfect assimilation by the organism is also needful, such objections to the generalisation not only disappear, but such a phenomenon as the coincidence of returning fertility with disappearing obesity affords a confirmatory argument.



A species of Onion with asexual vegetative bulbils (*b*) among the flowers (*a*).

Organisms having aberrant modes of life are next appealed to for crucial evidence bearing on these general doctrines. Thus, turning to vegetable and animal parasites, which combine superabundant nutrition with greatly diminished expenditure, the enormous fertility exhibited by all such forms is seen to be the necessary correlative of such a state of nutrition and expenditure, and not merely an acquired adaptation to their peculiar difficulties of survival. The reversion exhibited by so many species (especially among the higher arthropods, *e.g.*, *Aphis*, *Cecidomyia*) from sexual reproduction to primitive forms of genesis, is explained by pointing out that such species are peculiarly situated in obtaining abundant food with little exertion. Among bees, ants, and termites alike, the enormous fertility of the inactive and highly nourished queen-mother are obviously also cases in point.

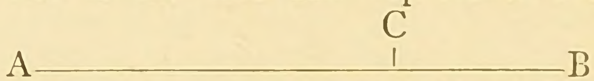
The inverse variation of genesis with individuation has now been demonstrated inductively as well as deductively, and that for each element of the latter (growth, development, or activity). Yet before discussing its application to the problems of the multiplication of the human species, two points remain,—a question has to be answered, and a qualification made. The question, only partially answered in course of the preceding argument, is, How is the ratio between individuation and genesis established in each special case? and the answer is, By natural selection. This may determine, whether the quantity of matter spared from individuation for genesis be divided into many small ova or a few larger ones ; whether there shall be small broods at short intervals,

or larger broods at longer intervals; or whether there shall be many unprotected offspring, or a few carefully protected by the parent. Again, survival of the fittest has a share in determining the proportion of matter subtracted from individuation for genesis. Yet this operation of natural selection goes on strictly under the limits of the antagonism above traced.

The needed qualification arises on introducing the conception of evolutionary change. If time be left out of account as hitherto,—or, what is the same thing, if all the species be viewed as permanent,—the inverse ratio between individuation and genesis holds absolutely. But each advance in individual evolution (it matters not whether in bulk, in structure, or in activities) implies an economy; the advantage must exceed the cost, else it would not be perpetuated. The animal thus becomes physiologically richer; it has an augmentation of total wealth to share between its individuation and its genesis. And thus, though the increment of individuation tends to produce a corresponding decrement of genesis, this latter will be somewhat less than accurately proportionate. The product of the two factors is greater than before; the forces preservative of race become greater than the forces destructive of race, and the species spreads. In short, genesis decreases as individuation increases, yet not quite so fast.

Hence every type that is best adapted to its conditions—every higher type—has a rate of multiplication that ensures a tendency to predominate. For though the more evolved organism is the less fertile absolutely, it is the more fertile relatively.

The whole generalisation admits of the simplest graphic illustration. For if the line AB represents the aggregate



matter or energies, the structures or the functions, of the organism, of which AC denotes the amount devoted to individuation and CB to reproduction, the inverse variation of AC to CB is obvious, as also if AC and CB represent the psychological obverse of these two classes of function. Nor does an increase in total energy modify this, as when the stronger members of a species frequently also exhibit greater reproductive power; for if in one case AB = 20, of which CB = 4, and in another AB = 25, CB may become 5 without any rise of reproductive ratio, since $\frac{4}{20} = \frac{5}{25}$. But if the species be evolving, the advance in individuation implies a certain economy, of which a share may go to diminish the decrement to genesis, as above explained.

§ 4. *Spencer's Application of his Results to Man.*—In extending this hard-won generalisation to the case of man, the concomitance of all but highest total individuation with all but lowest rate of multiplication (the enormous bulk of the elephant involving a yet greater deduction from genesis) is at once apparent. Comparing different races or nations, or even

different social castes or occupations, the same holds good; while the prevalence of high multiplication in races of which the nutrition is in obvious excess over the expenditure is also evident, witness the Boers or French Canadians. Such an apparent difficulty as that of the Irish, in whom rapid multiplication occurs despite poor food, is accounted for by the relatively low expenditure in obtaining it (since the "law of diminishing return" implies its converse for diminishing labour), though, no doubt, also in part by the habit of early marriage, if not by some measure of lowered individuation as well. The main position being established, Spencer proceeds to discuss the question of human population in the future, and insists strongly on the importance of pressure of population, which he regards as the main incentive to progress alike in past, present, and future. Reviewing the possibilities of progress in bulk, complexity of structure, multiplication and variation of function, he concludes that the more complete moving equilibrium, and more perfect correspondence between organism and environment, which such evolution involves, must take place mainly in the direction of psychical development. Yet this development, while stimulated by pressure of population, constantly tends to diminish the rate of fertility; in other words, this cause of progress tends to disappear as it achieves its full effect. The acute pressure of population, with its attendant evils, thus tends to cease as a more and more highly individuated race busies itself with its increasingly complex yet normal and pleasurable activities, its rate of reproduction meanwhile descending towards that minimum required to make good its inevitable losses.

§ 5. *Summary of the Population Question.*—The general question, so far as yet developed, may now be conveniently summarised in the accompanying tabular form. Here the stage of knowledge reached by each author, together with any practical applications therefrom deduced, may be read horizontally, while the historic development of each separate line of conceptions may be traced vertically.

From such a summary, brief as it is, the main steps in the development of our knowledge are clear enough, but a deeper analysis is required before final exposition or complete application is possible. Nor, when we note how vast the progress of science through the advance in precision and extension

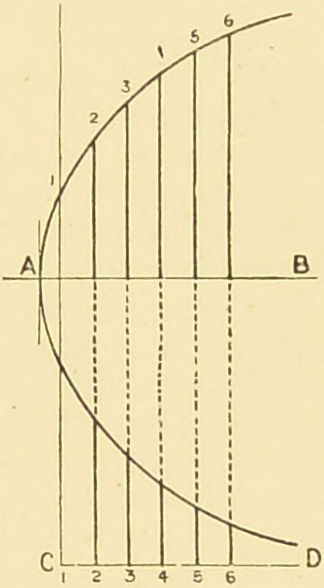
effected upon the conception of Malthus* by Darwin, will the utility of such increasing elaboration be disputed. Thus the full inductive verification of Spencer's law involves a detailed

Author.	Development of Theory of Population.			Practical Action Deduced.
I. Non-biological writers (predecessors and opponents of Malthus).	Increase of population does not tend to outrun subsistence.			
II. Malthus. 1798.	Increase of population tends to outrun that of subsistence.	But meets checks: A. Positive. B. Preventive.		To avoid A, adopt B.
III. Darwin. 1859.	Do.	Hence struggle for existence: A. Natural selection. B. Artificial selection.	Leading to evolution.	*Laissez-faire*, *i.e.*, on account of advantage to species from A, avoid B.
IV. Spencer. 1852-66.	Do. Rate of multiplication investigated for different species, and shown to vary inversely as individuation.	Do.	Do. Also leading to evolution of species.	Do. [*Individuate.*]

comparison of the rates of reproduction of each group of organic species, with their observed degree of individuation (first in each of its factors, and finally in their sum), deviations from the inverted symmetry of the theoretic curves (see fig. opposite) having to be separately discussed. Natural selection also requires a yet deeper analysis; the limits and possibilities of artificial selection are but little known, while

* It is also interesting to compare Malthus's view of population, tending to increase in geometrical proportion and substance only in arithmetical, with Spencer's demonstration of the limit of growth already summarised (see p. 220), the more so when we bear in mind that reproduction is discontinuous growth. The precise statement of Malthus becomes confirmed, as regards the cell, if not the cell aggregate.

a theory of variation is still far from agreed upon. If however we bear in mind that the amount of evolution in given time is but small our knowledge seems not insufficient for the practical deductions which are so pressingly demanded; yet it is here that the most serious disagreement has prevailed. Thus the Malthusian position is obviously inadequate, in not allowing for the Darwinian one; yet the converse also is undeniable, for the position of *laissez-faire*, upon which Darwin and Spencer alike take their stand, not only almost ignores the wellbeing of the individual in considering the advancement of the species, but is even then too optimistic, since it not only fails to accelerate the progressive evolution which is alone considered, but also fails to provide against the equal possibility of degenerative change. Are we then simply to return to the somewhat crude proposals and excessive hopes for the increase of individual wellbeing due to Malthus or his followers, based too as these have been on imperfect pre-Spencerian knowledge?



Let the perpendiculars above the line A B denote the increasing degree of total individuation of a series of forms 1, 2, 3, 4, 5, 6 (say Worm, Fish, Frog, Bird, Man, Elephant), and similarly let the perpendiculars to C D represent the rate of multiplication of the same forms; the curves joining these two series of points respectively illustrate by their inverted symmetry the inverse ratio of individuation and genesis.

The answer is not far to seek,—it lies in the generalisation above established; yet it is remarkable that Mr Spencer, after not only establishing the inverse variation of individuation and genesis among species in general, but even showing for the human species in particular that it is essentially upon increase of the psychical activities that the increased individuation and diminished genesis of the future must depend, should not have proceeded to a fuller application. For unless the main generalisation be abandoned, it is obvious that the progress of the species and of the individual alike is secured and accelerated whenever action is transferred from the negative side of merely seeking directly to repress genesis, to the positive yet indirect side of proportionally increasing individuation. This holds true of all species, yet most fully of man, since that modification of psychical activities in which his

evolution essentially lies, is *par excellence* and increasingly the respect in which artificial comes in to replace natural selection. Without therefore ignoring the latter, or hoping ever wholly to escape from the iron grasp of nature, we yet have within our power more and more to mitigate the pressure of population, and that without any sacrifice of progress, but actually by hastening it. Since then the remedy of pressure and the hope of progress alike lie in advancing individuation, the course for practical action is clear,—it is in the organisation of these alternate reactions between bettered environment (material, mental, social, moral) and better organism in which the whole evolution of life is defined, in the conscious and rational adjustment of the struggle into the culture of existence.

The practical corollaries of the Malthusian view are celibacy, late marriage, and moral control; the objections are vice, increased mortality in childbirth, and the present low evolution of our moral nature. The practical corollary of the Darwinian doctrine is virtually *nil;* the objection, that the survival of what we consider the best types is doubtful, and that the survival of the fit is apt to be cruel. The practical corollaries of the Spencerian principle, although Mr Spencer can hardly be said to have insisted upon these, are individuate and educate. The objection is, that the pressure of population is already felt, and that individuation is a matter of centuries. Furthermore, the effect of education, for instance in reducing sexuality, will tell most where it is least wanted, viz., among the best types.

We are therefore bound to include, as a continuation of the above table, the amendment of some of the most thoughtful exponents of what is generally called neo-Malthusian doctrine. This advocates the use of artificial preventive checks to fertilisation. Discussion of this proposal is at present difficult, because of the comparative absence of distinctly expressed opinion on the part of medical experts, and because of strong superficial prejudices, not only against the scheme, but against its discussion. These prejudices are, however, dying out, and that is well, for they do nothing but obscure appreciation alike of the merits and demerits of the doctrine. An increasing realisation of the plain facts of reproduction and population must rapidly exterminate the persistently theological absurdities which people utter, if they do not believe on the subject. The vague feeling that control of fertilisation is "interfering with nature," in some utterly unwarrantable fashion, cannot be

consistently stated by those who live in the midst of our highly artificial civilisation. The strongest prejudice seems to be based in a moral cowardice, which gauges a scheme by its "respectability," while even more culpable is that consciously or unconsciously derived from the profitableness to the capitalist classes of unlimited competition of cheap unskilled labour. For never did the proletariat more literally deserve its name than since the advent of the factory period, their rapid and degenerative increase, indeed, primarily representing "the progress of investments."

The general attitude of the modern Malthusian may first of all be roughly indicated by quoting the mottoes which head the organ of their league. "To a rational being, the prudential check to population ought to be considered as equally natural with the check from poverty and premature mortality" (Malthus, 1806). "Little improvement can be expected in morality until the production of large families is regarded in the same light as drunkenness, or any other physical excess" (John Stuart Mill, 1872). "Surely it is better to have thirty-five millions of human beings leading useful and intelligent lives, rather than forty millions struggling painfully for a bare subsistence" (Lord Derby, 1879). Starting from the familiar induction that "population has a constant tendency to outrun the means of subsistence," they recognise in this over-population "the most fruitful source of pauperism, ignorance, crime, and disease." To counteract this there are checks, positive or life-destroying on the one hand, prudential or birth-preventing on the other. "The positive or life-destroying checks comprehend the premature death of children and adults by disease, starvation, war, and infanticide." As these positive checks are happily reduced with the progress of society, attention must be concentrated on the other side. "This consists in the limitation of offspring by abstention from marriage, or by prudence after marriage." But as to the first, prolonged abstention from marriage, as advocated by Malthus, this is "productive of many diseases, and of much sexual vice," while "early marriage, on the contrary, tends to secure sexual purity, domestic comfort, social happiness, and individual health." The check that remains to be advocated is thus "prudence *after* marriage," and by this the neo-Malthusians most distinctly mean attention to methods which will secure that sexual intercourse be not followed by fertilisation. For

the details of the various methods, we must refer to the Malthusian literature; but a brief outline is imperative, even for an approximate understanding of the problem.

(*a.*) Thus we have the suggestion that intercourse should be limited to the relatively infertile period most remote from menstruation, when conception may indeed occur, but with less probability than at other periods. Although gynæcologists are disagreed as to the degree of this probability, there can be little doubt that such limitation would have a useful influence, although in itself confessedly incomplete. The so-called artificiality of control is here reduced to a minimum, and the suggestion is obviously in harmony with that increased temperance which all must allow to be desirable.

(*b.*) In the second place, there are methods employed by the males, such as that of withdrawal before the emission of the seminal fluid, a habit common enough both in savage and civilised communities. Fertilisation is in this way absolutely prevented, but apart from a more general objection to be afterwards emphasised, such a practice is maintained by some to be injurious to the male, and yet more to the female. Moreover, although the risks of over-population and female exhaustion by child-bearing are here minimised, there is still risk of male exhaustion.

(*c.*) Thirdly, although again under the severe criticism of some of the medical experts, there are means employed by the females, for securing by means of pessaries that the spermatozoa do not come into contact with the ovum, or by means of washes that the male elements are rendered ineffectual. In reply to the medical objections to both these methods of artificial check, it is answered (*a*) that it may in many cases be necessary to choose between two evils, of which the risk involved in the artificial check may be much less than that involved in continued child-bearing; (*b*) that it is hardly a fair argument *as yet* to urge that the proposed checks of neo-Malthusianism are fraught with danger. As to the popularly supposed preventive check of prolonged nursing one baby in the hope of thereby preventing a new conception, it is necessary to emphasise that nursing does *not* effect this, and that the prolongation of the lacteal function and diet beyond their natural limits is seriously injurious alike to mother and offspring.

Even recognising some of these objections, the neo-Malthusians urge the number of distinct advantages,—the reduction

of the present rapid rate of increase; the possibility of earlier marriages, and a probable diminution of vice; an increase in the fitness of the race by lessening the propagation of unfit types and the exhaustion of the mothers by too frequent child-bearing. Supposing, again, the general adoption of the proposal, the neo-Malthusians insist upon the possibility of a heightened standard of comfort among the poorer members of the community, and the removal of obstacles to marriage which stand in the way of those who ought to marry but ought not to be parents.

Without urging medical objections above referred to,—for in regard to the discussion of these, professional experts must bear the responsibility,—we must emphasise several counter-arguments. Thus it has been maintained, though with no great degree of certitude, that a proposal involving some deliberate and controlled action would tend to be adopted most where least wanted, viz., among the more individuated types, whose numbers would in consequence be proportionately reduced. The diminished rate of increase, which is the most obvious social result of the extensive adoption of neo-Malthusian practices, has long been known to the student of population; and in some countries, particularly France,—although here, no doubt, to some extent the result of peculiarly high individuation,—is a recognised national danger, especially since the diminished population, in being largely freed from the normal acuteness of the struggle for existence, loses many of the advantages of this as well.

The statistician will doubtless long continue his fashion of confidently estimating the importance and predicting the survival of populations from their quantity and rate of reproduction alone; but at all this, as naturalists we can only scoff. Even the most conventional exponent of the struggle for existence among us knows, with the barbarian conquerors of old, that "the thicker the grass, the easier it is mown;" that "the wolf cares not how many the sheep may be." It is the most individuated type that prevails in spite, nay, in another sense, positively because of its slower increase; in a word, the survival of a species or family depends not primarily upon quantity, but upon quality. The future is not to the most numerous populations, but to the most individuated. And as we increasingly see that natural history must be treated primarily from the standpoint of the species-regarding sacrifice rather than

from that of the individual struggle, we see the importance of the general neo-Malthusian position, despite the risks which the particular modes of its practice may involve.

Apart from the pressure of population, it is time to be learning (1) that the annual childbearing still so common, is cruelly exhaustive to the maternal life, and this often in actual duration as well as quality; (2) that it is similarly injurious to the standard of offspring; and hence (3) that an interval of two clear years between births (some gynæcologists even go as far as three) is due alike to mother and offspring. It is time therefore, as we heard a brave parson tell his flock lately, "to have done with that blasphemous whining which constantly tries to look at a motherless" (ay, or sometimes even fatherless) "crowd of puny infants as a dispensation of mysterious providence." Let us frankly face the biological facts, and admit that such cases usually illustrate only the extreme organic nemesis of intemperance and improvidence, and these of a kind far more reprehensible than those actions to which common custom applies the names, since they are species-regarding vices, and not merely self-regarding ones, as the others at least primarily are. To realise the social consequences of sexual intemperance is enough to obviate any hasty criticism of neo-Malthusianism, whatever conclusion may be arrived at as to its sufficiency.

It is time, however, to point out the chief weakness in neo-Malthusian proposals, which are at one in allowing the gratification of sexual appetites to continue, aiming only at the prevention of the naturally ensuing parentage. To many doubtless the adoption of a method which admits of the egoistic sexual pleasures, without the responsibilities of childbirth, would multiply temptations. Sexuality would tend to increase if its responsibilities were annulled; the proportion of unchastity before marriage, in both sexes, could hardly but be augmented; while married life would be in exaggerated danger of sinking into "monogamic prostitution." On the other hand, it seems probable that the very transition from unconscious animalism to deliberate prevention of fertilisation, would tend in some to decrease rather than increase sexual appetite.

It seems to us, however, essential to recognise that the ideal to be sought after is not merely a controlled rate of increase, but regulated married lives. Neo-Malthusianism might secure the former by its more or less mechanical methods, and there is no doubt that a limitation of the family would often increase

the happiness of the home; but there is danger lest, in removing its result, sexual intemperance become increasingly organic. We would urge, in fact, the necessity of an ethical rather than of a mechanical "prudence after marriage," of a temperance recognised to be as binding on husband and wife as chastity on the unmarried. When we consider the inevitable consequences of intemperance, even if the dangers of too large families be avoided, and the possibility of exaggerated sexuality becoming cumulative by inheritance, we cannot help recognising that the intemperate pair are falling towards the ethical level of the harlots and profligates of our streets.

Just as we would protest against the dictum of false physicians who preach indulgence rather than restraint, so we must protest against regarding artificial means of preventing fertilisation as adequate solutions of sexual responsibility. After all, the solution is primarily one of temperance. It is no new nor unattainable ideal to retain, throughout married life, a large measure of that self-control which must always form the organic basis of the enthusiasm and idealism of lovers. But as old attempts at the regulation of sexual life have constantly fallen from a glowing idealism into pallor or morbidness, it need hardly be said that the same fate will ever more or less befall the endeavour after temperance, so long as that lacks the collaboration of other necessary reforms. We need a new ethic of the sexes; and this not merely, or even mainly, as an intellectual construction, but as a discipline of life; and we need more. We need an increasing education and civism of women,—in fact, an economic of the sexes very different from that nowadays so common, which, while attacking the old co-operation of men and women because of its manifest imperfections, only offers us an unlimited and far more mutually destructive industrial competition between them instead. The practical problems of reproduction become in fact, to a large extent, those of improved function and evolved environment; and limitation of population, as we are beginning to see in regard to the more individual forms of intemperance, is primarily to be reached, not solely by individual restraint, but by a not merely isolated and individual, but aggregate and social, reorganisation of life, work, and surroundings. And while our biological studies of course for the most part only point the way towards deeper social ones, they afford also one luminous principle towards their prosecution,—that thorough

parallelism and coincidence of psychical and material considerations, upon which moralist and economist have been too much wont respectively to specialise.

§ 6. *Rate of Reproduction "Nil"—Sterility.*—When we view reproduction in terms of discontinuous growth,—that is, as a phenomenon of disintegration,—it is obvious that complete integration of the matter acquired by the organism into its own bulk, and for its own development, precludes reproduction,—that is, involves sterility,—and similarly as regards the energies of the organism. This is only a re-statement of Spencer's generalisation above discussed; for it is evident that, if genesis vary inversely as individuation, it must be suppressed altogether if individuation becomes complete. The actual phenomena, however, by no means usually admit of explanation as such realisations of the ideal of evolution, and hence the cause and treatment of sterility mainly pass into the provinces of the experimental naturalist and the physiological physician. From the earliest times, indeed, physician and naturalist, priest and legislator, alike devoted attention to the subject; and it was probably in this way, as a recent monographer remarks, that research became directed to the larger problem of reproduction in general. The general biological questions—*e.g.*, the relations between sterility within the limits of a species to changes in the environment, or that of sterility among hybrids — are extensively discussed in the copious literature which centres around Darwin's "Variation of Animals and Plants under Domestication"; while with regard to the human species, an extensive medical literature of course exists, to which any encyclopædia of medicine, or conveniently the recent careful monograph of P. Müller (" Die Unfruchtbarkeit der Ehe," Stuttgart, 1885), will furnish bibliographical details.

SUMMARY.

1. The rate of reproduction is chiefly determined by the constitution of the organism; the rate of increase, by its relations to the animate and inanimate environment.

2. The naturalist has to thank the sociologist for directing emphatic attention to the laws of multiplication.

3. Summary of Spencer's analysis. Individuation and genesis vary inversely.

4. In regard to man, Spencer urges the importance of pressure of population as an incentive to progress, and concludes that man's future evolution must continue mainly in the direction of psychical development, and predicts with the increase of individuation a diminution of fertility.

5. Predecessors and opponents of Malthus denied that increase of population tended to outrun subsistence; Malthus successfully demonstrated his thesis, and noted the checks which curbed the increase; Darwin emphasised the advantage of the pressure and checks; Spencer shows the inverse ratio of degree of development and rate of reproduction; neo-Malthusians advocate the use of artificial preventive checks to fertilisation. Discussion of these various generalisations and proposals.

6. Completed individuation, were that possible, would be theoretically associated with sterility.

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CHAPTER XXI.

The Reproductive Factor in Evolution.

§ 1. *General History of Evolution.*—The history of the doctrine of evolution is essentially modern; for though the idea glimmered before the minds of many ancient philosophers from Empedocles to Lucretius, it was not till the eighteenth century that naturalists began seriously to apply the conception to the problem of the origin of our fauna and flora. In thinking of the history, it is necessary to distinguish, on the one hand, the gradual growth of the conviction that the theory of evolution is a satisfactory modal interpretation of the origin of animate nature as we know it, and, on the other, the inquiry into the real mechanism of the process. The value of the evolution doctrine as a thought-economising formula was made quite clear by the labours of Spencer, Darwin, Wallace, Haeckel, and others; the real ætiology of organisms, the "how" of the evolution process—is still the subject of searching inquiry and keen debate.

The idea of evolution, for so many centuries a latent germ, first took definite shape, so far as biology is concerned, in the mind of Buffon (1749), who not only urged the general conception with diplomatic skill and powerful irony, but sought to elucidate the working out of the process. He illustrated the influence of new conditions in evoking new functions; showed how these in turn reacted upon the structure of the organism; and how, most directly of all, changes of climate, food, and other elements of the environment, were external factors evoking internal change, whether for progress or for degeneration.

Contrasted with Buffon in many ways, both in his mode of treatment and in his view of the factors, was Erasmus Darwin (1794), the grandfather of the author of the "Origin of Species." In rhyme and reason, with all the humour and common-sense of a true Englishman, and with a vivid appreciation of life as

more than mechanism, he stated the general conception of evolution, and emphasised the organism's inherent power of self-improvement, the moulding influence of new needs, desires, and exertions, and the *indirect* action of the environment in evoking these.

To Treviranus (writing in 1802-31)—a biologist too much neglected both in his lifetime and since—organisms appeared almost indefinitely plastic, especially however under the direct influence of external forces. His keen analysis of possible factors did not fail to recognise—what Brooks, Galton, Weismann, and others have since elaborated—that the union of diverse sexual elements in fertilisation was in itself a fountain of change. "Every form of life," he says, "may have been produced by physical forces in either of two ways, either from formless matter, or by the continuous modification of form. In the latter case, the cause of change may be either in *the influence of the heterogeneous male reproductive matter on the female germ*, or in the influence of other potencies after generation."

His contemporary Lamarck (writing in 1801-9)—of greater posthumous fame—fought in poverty like a hero for the evolutionary conceptions of his later years. He is well known to have emphasised the importance of changed conditions in evoking new needs, desires, and activities, urging at the same time the perfection wrought upon organs by increased practice, and conversely the degeneration which follows as the nemesis of disuse. As regards the evolution of plants, he laid the main emphasis on the modifications brought about by the environment. Evolution seemed to him to be due to the interaction of two fates,—an internal progressive power of life; and the external force of circumstances, encountered in the twofold struggle with the inanimate environment and with living competitors. The keynote of his system was that adaptive modifications in the bodies of organisms are brought about by changes in function or in environment, or in both, and that these modifications are in some degree at least inheritable.

Among the philosophers too, and especially in the minds of those who had been disciplined in physical or historical investigations, the speculations of the ancients were ever taking fresh form, gaining moreover in concreteness. Thus Kant viewed the evolution of species mainly in terms of the mechanical laws of the organism itself, but allowed also for

the influence of environment, noted the importance of selection in artificial breeding, and, like such ancients as Empedocles and Aristotle, had glimpses of the notion of the struggle for existence. The same idea is more distinct in Herder's "Philosophy of History," where, probably under Goethe's influence, he speaks of the "struggle, each one for itself, as if it were the only one," of the limits of space, and of the gain to the whole from the competition of individuals. Oken (1809) saw the light of the evolution idea dancing like a will-o'-the-wisp in the mist of his "Urschleim" speculations, and seemed chiefly to interpret the organic progress in terms of action and reaction between the organism and its surroundings; while in the noble epic of evolution which we owe to his contemporary Goethe, the adaptive influence of the environment and the inherent growth-tendencies of the organism are especially emphasised.

Wells in 1813, and Patrick Matthew in 1831, forestalled Darwin in suggesting the importance of natural selection; but their virtually buried doctrines, however interesting historically, were of less practical importance than those of Robert Chambers, the long unknown author of the "Vestiges of Creation" (1844-53). His hypothesis of evolution emphasised the growing or evolving powers of the organisms themselves, which developed in rhythmic impulses through ascending grades of organisation, modified at the same time by external circumstances, which acted with most effect on the generative system. It is difficult indeed to refrain from amusement or irritation at the naïve simplicity with which he evolves a mammal from a bird, by the short and easy method of prolonging the period of uterine life in favourable nutritive conditions; but though a goose could not so simply give rise to a rat, the emphasis laid on the influence of prolonged gestation is full of suggestion. Apart from his common-sense view of evolution as a process of continued growing, Chambers deserves to be remembered as one of the first to appreciate "the force of certain external conditions operating upon the parturient system."

In France, Etienne and Isidore Geoffroy St Hilaire—father and son—denied indefinite variations, regarded function as of secondary importance, and laid special stress upon the direct influence of the environment. To them it seemed not so much the effort to fly, as the (supposed) diminished proportion

of carbonic acid in the atmosphere, which had determined the evolution of birds from ancient reptiles. A complete history of evolution theories, up to the publication of the "Origin of Species" (1859), would have to take account further of the opinions of the geographer Von Buch and the embryologist Von Baer, of Schleiden and Naudin, Owen and Carus, and many others; but no such survey is here our purpose.

For it must be already evident from the above brief sketch of representative opinions, that successive naturalists have emphasised now one factor and now another in the evolutionary process. To one it seemed as if the organism had a motor power of development—often a metaphysical one, it must be allowed—within itself, and that evolution was to be explained, in Topsian fashion, "according to the laws of organic growth;" to another, function appeared all-important, perfecting organs on the one hand, allowing them to wane in disuse on the other; to a third, organisms were seen under the hammers of external forces and circumstances, being continuously welded into more and more perfectly adapted forms. The intrinsic character of the organism, its function, and its environment, on each of the three factors emphasis was in turn laid.

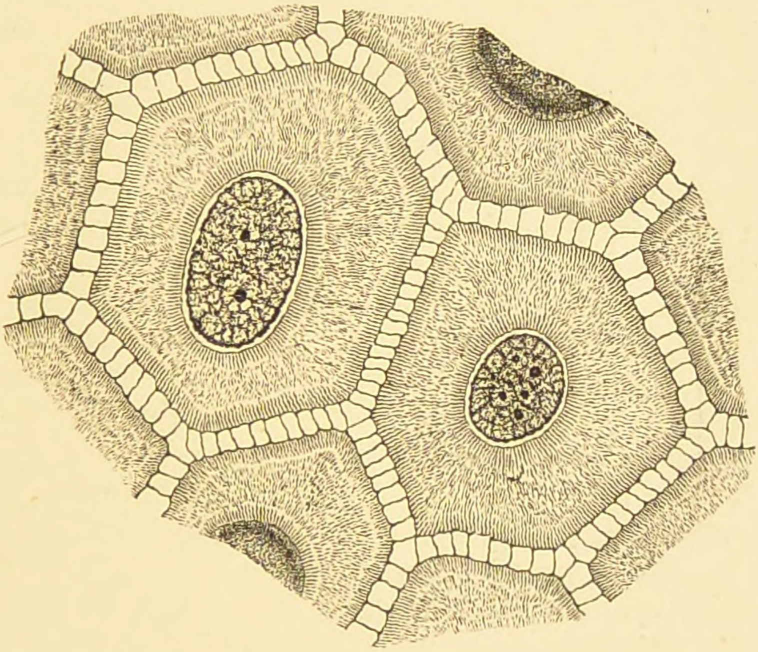
At this juncture Darwin elaborated his theory of "The Origin of Species by means of Natural Selection and the Preservation of Favoured Races in the Struggle for Life," and was independently and simultaneously corroborated by Alfred Russel Wallace. They did not indeed deny a spontaneous power of change in the organism itself, nor the influence of function and environment; but, without definitely discussing the origin of variations, sought to show how the destructive or eliminating, and the conservative or selecting agency of the animate and inanimate environment, were the directive factors in evolution. Given a sufficient crop of indefinite variations, —unanalysed or unanalysable as to their origin,—the struggle for existence separated the minority of wheat ears from the majority of tares, and secured a finer and finer harvest.

So much had Darwin in his magistral labours to do with making the general conception of evolution current coin, that we can readily understand how not only the educated laity, but the majority of professed naturalists, identified their adherence to the general doctrine with a subscription to the specific principle of natural selection, and in becoming evolu-

tionists became at the same time Darwinians, that is to say, natural selectionists. Of late years, however, as conflict has passed from the outworks to the very citadel of evolution,—has come, that is to say, to centre round the problem of the origin of variations,—history has repeated itself. Naturalists such as Nägeli, Mivart, and Eimer have championed the cause of internal organismal variations, of evolution in terms of the constitution of the organism, of progress according to the definite laws of organic growth. An active school of neo-Lamarckians, such as Cope and Packard, has arisen in America; while Spencer has re-emphasised the importance both of function and of environment as factors in organic evolution, supported moreover in this position by the experimental work of Semper and others. The last published essays of Spencer may be referred to in illustration of the unended state of the controversy, but at the same time, of the growing tendency to limit the importance of natural selection, and as a good instance of successful endeavour to recognise the measure of truth in the different theories. Wallace remains staunchest among the upholders of the theory of natural selection, for his share in which he seems ever to refuse to take to himself sufficient credit; but it is interesting to notice, that in his "Darwinism" (1889), in re-inforcing his old objections against the importance which Darwin attached to sexual selection, he has made admissions welcome to those of us who believe that the shoulders of natural selection have also been overburdened. As we have already noticed, the phenomena of male ornament are discussed and summed up as being "due to the general laws of growth and development," so that it is "unnecessary to call to our aid so hypothetical a cause as the cumulative action of female preference." Again, "if ornament is the natural product and direct outcome of superabundant health and vigour,"—a view to which the reader of the preceding pages can be no stranger,—"then no other mode of selection is needed to account for the presence of such ornament." But if the origin of characters so important as those often possessed by males is to be ascribed to internal constitution rather than to the external selection of indefinite variations, the suggestion seems obvious that the origin of this, that, and the other set of characters may also be explained in the same way. A vivid historical account of the evolution of evolution-theory will be found in Osborn's "From the Greeks to Darwin," but a much larger work will be neces-

sary if justice is to be done to many who have contributed to working out the most characteristic idea of the nineteenth century. Thus Stuart-Glennie's insight in seeking to bring the laws of inorganic processes into line with the processes of organic evolution has never received due recognition.

Before we conclude this historical sketch, we must however refer to the subject of debate re-opened by Weismann, to whom, as one of the foremost of European naturalists, the reader's attention has already been so frequently directed. To a very large extent at least, we and our fathers have believed that characters acquired by the individual organism from



Two adjacent animal cells, showing communications through adjacent intercellular substance; also the protoplasmic network, and the nucleus.—After Pfitzner.

functional or environmental conditions might be transmitted as a legacy to the offspring. According to Weismann, and not a few others independent of and dependent on him, this has been a delusion. Not only is positive proof of such transmission of *acquired* characters, *i.e.*, other than those of constitutional, congenital, or germinal origin, so scanty and unsatisfactory that His has not hesitated to call the catalogue of cases a mere "handful of anecdotes," but the connection between the body-cells and the sex-elements seems to Weismann and his school so far from close or dependent, that there is a great probability

against any "somatic" modification specifically and representatively affecting the reproductive elements,—or, what comes to the same thing, the offspring. If the reproductive elements, in spite of the close connection between all parts of the body, or even between cell and cell (see above fig.), are unaffected directly and specifically by changes in the other parts of the body, then the functional and environmental "modifications" of the body, however important to the individual, are only of indirect importance in the evolution of the race. It has been suggested by Baldwin, Osborn, and Lloyd Morgan that advantageous modifications may serve in the struggle for existence as an individual shield until such time as congenital and therefore transmissible variations in the same direction may be established; but even if this be demonstrated, it remains true that the evolutionary importance of modifications is indirect. If individually acquired characters or "modifications" are of importance only to the individual body, they are obviously of no direct moment in the evolution of the species,—above the level of the Protozoa at least; and, as Weismann himself says, the ground is thus taken from under the feet of Buffonians, Lamarckians, neo-Lamarckians, etc. The ground is left clear for natural selectionists, and the struggle for existence acting on variations remains as the chief factor in the mechanism of evolution. Though we cannot demonstrate that a logical possibility has been the *vera causa* of past evolution, much has been done to establish the probability. But much still requires to be done by actual observation in the present to show that *discriminate* elimination is of frequent occurrence, for it is on the assumption of discriminate, as opposed to indiscriminate, elimination that the case for natural selection rests. To the question, What starts these variations which natural selection eliminates or fosters? Weismann has suggested various answers:—(*a*) That the action of the environment on the bodiless Protists established a multitude of differences of which all subsequent variations in the multicellular organisms are simply permutations and combinations; (*b*) that a prolific source of variation is to be found in the intermingling or amphimixis of the sex-cells in fertilisation, and in the reduction-processes associated with the maturation of these sex-cells; and (*c*) that the germ-plasm is provoked to vary by nutritive and other stimuli acting on it from without, or from the enclosing body of the parent-organism. There are many, however, who would

still say, that even if none but constitutional or germinal variations are transmissible, we are not shut up to the exclusive adoption of the natural selectionist position. It is still open to the naturalist to demonstrate that many adaptations at least are not explicable as the result of a long process of fostering and eliminating selection among a host of sporadic indefinite variations, but are rather the direct and necessary results of "laws of growth," of "constitutional tendencies," or of the precise chemical nature of the protoplasmic metabolism in the organisms in question. If constitutional variations occur along a few definite lines, as Eimer, Geddes, and others have maintained in certain cases, then we can understand the origin, though not perhaps the distribution, of species apart from any long process of selection, for which indeed, if variations be strictly definite, the material must be vastly reduced. In other words, we can think of the organism not merely under the moulding influence of its functions, nor solely as the product of environmental hammering, least of all as the survivor from a crowd of unsuccessful competitors, but as the expression of an internal fate, no longer mystical, but expressible in terms of the dominant chemical constitution.

§ 2. *The Reproductive Factor.*—Without further discussion of the still open controversy as to the various factors of evolution, which would not be relevant to such a work as this, we must summarily collate the more prominent opinions as to the share reproduction has in the process. To most of these we have already alluded in the body of the book.

(*a.*) First of all, as to the origin of variations, we find that what Treviranus recognised in the first years of this century—viz., the influence of fertilisation in evoking change—has been emphasised by several, such as Brooks and Galton, and has been especially elaborated by Weismann. As we have already noted, Weismann has suggested that the intermingling of two "germ-plasmas," which is at least part of the essence of fertilisation, may be an important fountain of congenital variations. In apparent contrast is the view advocated by Hatschek, who sees in the intermingling essential to fertilisation a counteractive of idiosyncrasies, a means of controlling and checking disadvantageous individual peculiarities. The two positions are not antagonistic, but rather complementary.

(*b.*) No impartial student of Darwinism can fail to admit, that in the "struggle for existence" stress is laid upon the

nutritive and self-maintaining functions and strivings, yet we must remember Darwin's own words:—"I should premise that I use this term [struggle for existence] in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny" ("Origin of Species," p. 50). Similarly, Herbert Spencer says: "If we define altruism as being all action which, in the normal course of things, benefits others instead of benefiting self, then from the dawn of life altruism has been no less essential than egoism. Though primarily it is dependent on egoism, yet secondarily egoism is dependent on it." "Self-sacrifice is no less primordial than self-preservation" ("Principles of Ethics" and "Principles of Psychology").

(*c.*) Darwin also insisted upon the *rôle* of "sexual selection," which implies a recognition of the reproductive factor. We have seen, however, that sexual selection is only a special case of natural selection; that it seeks to explain the elaboration, not the origin of sexual peculiarities; and lastly, that Darwin's arguments in favour of the mechanism which he emphasised, have been seriously impugned by Wallace, in an attack which reacts strongly upon the critic's own position. It must not be overlooked, however, that the existence of any form of selective, as opposed to indiscriminate mating, will, if natural selection be at work, tend to accelerate the process of differentiation. (See Pearson's "Grammar of Science," 2nd edition, 1900, pp. 423-437.)

(*d.*) Romanes has recently elaborated, what others seem also to have suggested, the importance of mutual sterility in splitting up one species into several. "Whenever any variation in the highly variable reproductive system occurs, tending to sterility with the parent form without impairing fertility with the varietal form, a physiological barrier must interpose, dividing the species into two parts, free to develop distinct histories, without mutual intercrossing, or by independent variation." The reproductive system is very apt to vary,—why, he does not say; the consequence might readily be, that among the progeny of a parent stock some were fertile *inter se*, but infertile with the consistent members of the parent stock; these will be isolated by a physiological barrier, just as they might be insulated by a geographical one, and left free to develop along divergent paths of their own. Here

again there is recognition of the reproductive factor in evolution; but how far, and in what cases species have so originated, is obviously a question which would involve discussion of each individual instance.

(*e.*) When pairing is restricted in its range to more or less closely related forms—*i.e.*, when inbreeding is practised—it seems to have up to a given limit the effect of fixing characters and developing prepotency. By prepotency is meant a relative strength in the power of transmitting character, or, in other words, the strong persisting power which certain characters have over others in inheritance. Thus if a certain character of a sire is invariably transmitted to the offspring, irrespective of the character of the dam, we say that the male is prepotent as regards that character. But if inbreeding occurs in nature —*e.g.*, as the result of some form of isolation, as it does in domestication; and if it has as one of its results the development of prepotency, we have here an important factor in evolution. For the prepotency will account for the persistence of variations in their early stages. (See "The Penycuik Experiments," by Professor J. Cossar Ewart, London, 1899, xciii. and 177 pp., 46 figs.)

(*f.*) There is among organisms, and even in allied species, an enormous variety in the actual fertility and in the potential fertility (fecundity); even among members of the same species there are great differences. The importance of this is increased when we note that Professor Karl Pearson, with the assistance of Miss Alice Lee and Mr. Leslie Bramley-Moore, have shown that fertility is *inherited* in man and fecundity in the horse—a conclusion which probably admits of great extension. The fact gives basis to Pearson's theory of "reproductive or genetic selection"—a phrase which he uses to describe the selection of predominant types owing to the different degrees of reproductivity being inherited, and without the influence of a differential death-rate. If fertility is inherited, and if fertility is correlated with other characters, there will be a continual tendency to progress in a definite direction, unless there be some counteracting factor which takes the form of a differential death-rate more intense for the offspring of the more fertile. ("Proc. Roy. Soc. London," lxiv., 1899, pp. 163-167.)

(*g.*) Worthy of consideration is the suggestion of Robert Chambers, crudely illustrated as it may have been, that environmental influences acted with special power upon the

generative system, and that the prolongation of gestation was a maternal sacrifice which brought its own reward in the higher evolution of the offspring. With this Beard's interesting essay on "The Span of Gestation" may be profitably compared. Miss Buckley has well pointed out how the increase of parental care was a factor in, as well as a result of, the general ascent; how the success of birds and mammals especially must in part be interpreted in reference to the noteworthy deepening of parental affection, and strengthening of the organic and emotional links between mother and offspring. In emphasising the progressive value of prolonged infancy, especially in the evolution of the emotions, Fiske has also recognised the importance of the reproductive factor. The same idea is prominent in Drummond's "Ascent of Man."

§ 3. *Further Construction.*—The general tendency of all theories of evolution has been to start with the individual organism as the unit, and to consider the self-maintaining and nutritive activities as primary, the reproductive and species-regarding as only secondary. But along many lines of research, such as those indicated in the preceding paragraphs, the importance of the reproductive factor has been recognised, and the centre of gravity of the evolutionary inquiry has already been to some degree shifted. Recent investigations on heredity, for instance, forbid that attention should any longer be concentrated on the individual type, or reproduction regarded as a mere repetition process; the living continuity of the species is seen to be of more importance than the individualities of the separate links. Physiologists and evolutionists are coming to see the most complex individual lives, in Foster's phrase, as "but the bye-play of ovum-bearing organisms." The species is a continuous undying chain of unicellular reproductive units, which indeed build out of and around themselves transient multicellular bodies, but the processes of nutritive differentiation, and other individual developments, are secondary, not primary.

Thus it is the central generalisation of botany that, despite the individual differentiation of fern, selaginella, cycad, conifer, and flower, these turn out, on deepest analysis, to be but the surviving phases of a continuous and definite increase in the subordination of the sexual parents to their asexual offspring.

Or if we take in particular the origin of the flower, which many botanists agree in regarding as a shortened branch, the

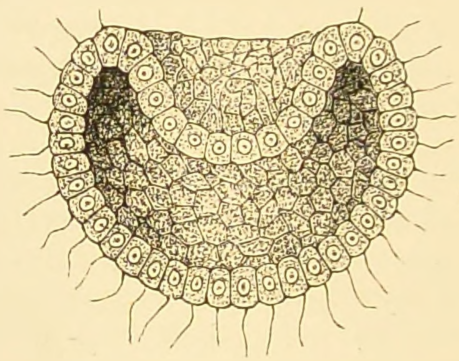
natural selectionist explanation would seem to be, that the flower had arisen by selection from the two other alternatives of lengthened and unshortened axes. But this point of view must be corrected in relation to the physiological theory that shortening of the axis was *inevitable*, since the expense of the reproductive functions necessarily checks the vegetative ones. It is evident that we cannot speak of *selection* where the imaginable alternatives are physically impossible. So too the shortening of the inflorescence from raceme to spike or flower-head, or still further into the hollowed form of a fig, with the corresponding reduction in the size of the flowers, is again the result of the check imposed by reproduction on the growth of axis and appendages.

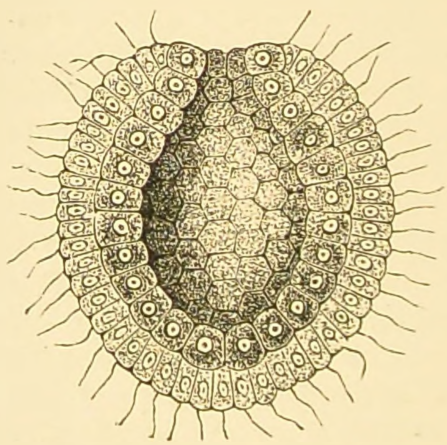
The same simple conception of a continuous checking of vegetation by reproduction unlocks innumerable problems of floral structure, large and small alike, from the inevitable development of gymnosperm into angiosperm by the continuous subordination of the reproductive carpellary leaf, to the variations of cabbages as seen in the transitions between leafy kale and cauliflower. Or again, the origin of floral colour, as primarily an inevitable consequence of the same principle of vegetative subordination through reproductive sacrifice, was long ago pointed out by Spencer, and admits of detailed elaboration without attaching more than secondary importance to selection by insects.

In another way, the antithesis between reproduction and nutrition may be illustrated among the existing orders and species of flowering plants. Just as the lilies, for instance, range on the one side towards the characteristically vegetative grass, or on the other towards the reproductive orchid, so it is with the main variations of every natural alliance. Thus, the Ranunculaceæ have their grassy and their orchid-like types in meadow-rue and larkspur respectively, while the species of these very genera show, within narrower limits, similar swings of variation. What we call higher or lower species are thus the leaders or the laggards along one or other of these two lines of variation.

Among animals, the importance of the reproductive factor may be illustrated in the most diverse series. Thus the greatest step in organic nature, that between the single-celled and many-celled animals, bridged as it is by loose colonies, some of which are at a very low morphological level, is not

due to the selection of the more individuated and highly adapted forms, but to the union of relatively unindividuated cells into an aggregate, in which each becomes diminishingly competitive and increasingly subordinated to the social whole. The colonial or multicellular forms, originating pathologically in all probability, may of course have rapidly justified their existence in the struggle for existence, just as unions of many kinds do in human society, but the Protozoa cannot be accused


(a)


(b)

Formation of the Gastrula.—From Haeckel.

of any prevision of future advantage in remaining clubbed together in co-operation, nor indeed credited with much primitive altruism in so doing.

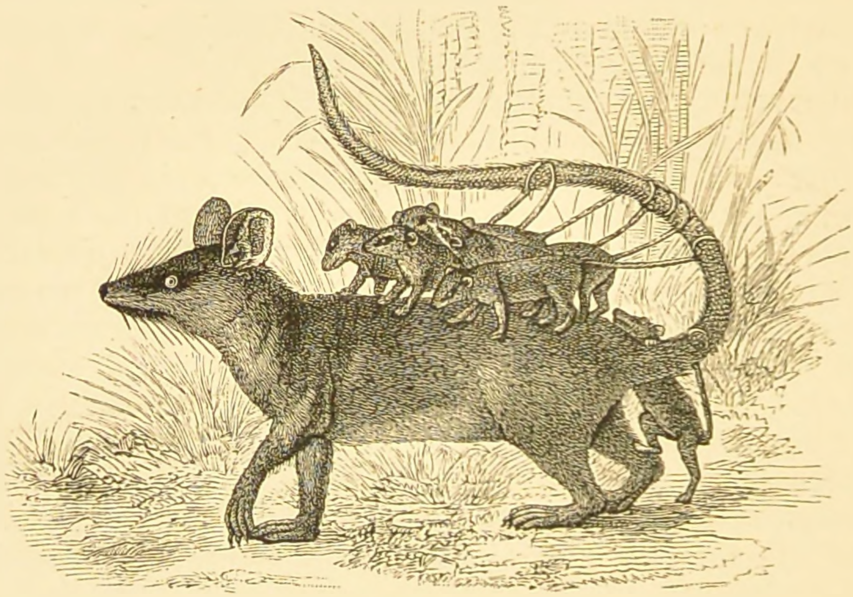
No structure is more emphatically nutritive in its adult result than the gut-cavity of the embryonic gastrula. It is worth inquiring whether this important step in differentiation was attained in history in response to nutritive needs. The usual supposition is certainly that the gastrula cavity, by whatever peculiarities of growth it may have arisen, justified itself

from the first in an additional nutritive advantage. But Salensky, in his studies on the primitive form of the Metazoa, has given strong arguments in favour of the theory that the primitive cavity, arising in a volvox-like form, was originally a brood-cavity or "genitocœl," and that it only secondarily acquired nutritive significance. It would be indeed striking if this important morphological step in the establishment of the nutritive system was reached along the road of reproductive modification; for if this most fundamental of nutritive and self-maintaining advantages, the belly itself, be but a secondary resultant of an originally reproductive and species-regarding progress, the lower Utilitarianism, which has so long been arguing from economics to biology and back again, is evidently a step nearer exposure.

Or again, that increase of reproductive sacrifice, which at once makes the mammal and marks its essential stages of further progress through oviparous monotreme, prematurely-bearing marsupial, and various grades of placental; that increase of parental care; that frequent appearance of sociality or co-operation, which even in its rudest forms so surely secures the success of the species attaining it, be it mammal or bird, insect or even worm,—all these phenomena of survival of the truly fittest, through love, sacrifice, and co-operation, need far other prominence than they could possibly receive on the hypothesis of the essential progress of the species through internecine struggle of its individuals at the margin of subsistence Each of the greater steps of progress is in fact associated with an increased measure of subordination of individual competition to reproductive or social ends, and of interspecific competition to co-operative association.

The corresponding progress in the historic and individual world, from sex and family up to tribe or city, nation and race, and ultimately to the conception of humanity itself, also becomes increasingly apparent. Competition and survival of the fittest are never wholly eliminated, but reappear on each new plane to work out the predominance of the higher, *i.e.*, more integrated and associated type, the phalanx being victorious till in turn it meets the legion. But this service no longer compels us to regard these agencies as the essential mechanism of progress, to the practical exclusion of the associative factor upon which the victory depends, as economist and biologist have too long misled each other into doing. For

we see that it is possible to interpret the ideals of ethical progress, through love and sociality, co-operation and sacrifice, not as mere utopias contradicted by experience, but as the highest expressions of the central evolutionary process of the natural world. The ideal of evolution is indeed an Eden; and although competition can never be wholly eliminated, and progress must thus approach without ever completely reaching its ideal, it is much for our pure natural history to recognise that "creation's final law" is not struggle but love. The fuller working out of this thesis, however, would lead us far beyond our present limits, towards a restatement of the



An Opossum (*Didelphys dorsigera*) carrying its young on its back.—From Carus Sterne.

entire theory of organic evolution. Suffice it here, in conclusion, to indicate an important change in the general point of view. The older biologists have been primarily anatomists, analysing and comparing the form of the organism, separate and dead; however incompletely, we have sought rather to be physiologists, studying and interpreting the highest and intensest activity of things living. From the study of individual structure they were wont to pass, indeed, to that of reproductive structures, and thence even functions; hence, too, the pair and the totality of the species did at length come successively into view, but this with the individualistic theory of natural

selection bulking as practically all-important in the foreground. For us, however, this perspective has become entirely reversed. The individual is a mere link in the species, and its reproductive processes are thus of fundamental importance to the interpretation even of its self-maintaining ones. Hence we no longer regard, with Darwin and the majority of our brother naturalists, the operation of natural selection upon individual characters as the simplest of problems, looking for residual explanation to sexual selection, and only in extreme difficulty invoking the aid of "principles of correlation," "laws of growth," and the like, viewed as almost inscrutably mysterious. On the contrary, it is the continual correlation yet antithesis—the action and reaction—of vegetative and reproductive processes in alternate preponderance, which seems to us of fundamental importance, since to this the general rhythm of individual and racial life runs fully parallel. Hence it is that we have the primeval lily developing on the one hand the ideally vegetative grass, yet also the supremely specialised reproductive orchid; and that we can trace (as we hold) the same swing of divergent evolution, of definite variation, in every natural order, nay, in every genus, often even in the very varieties of a species. Hence, too, it is that the rhythm of hydroid and medusoid in the individual life of the typical forms becomes fixed in coral or ctenophore as a racial temperament. This preponderance of passivity or activity (which we can read throughout, in barnacle and insect, as well as in tortoise and swallow) once set up, goes on accumulating till it meets reversal through environment or other causes, and limitation or extinction through the agency of natural selection, which, however, is more frequently a retarding force than an accelerant of evolution. The problem of organic progress is thus to be interpreted not merely as on conventional lines, by help of an analogy derived from an age of mechanical progress which gives us the watch, or sewing-machine, or tricycle,—by the cumulative patenting, as it were, of useful improvements in detail. The essential problem is not one of mechanism but of character, to which incident is accessory but not fundamental,—not of details put together, but of aggregate organic life or temperament. The life of the individual or the species is essentially a unity, of which the specific characters are but the symptoms, be their subsequent measure of importance and utility in adaptation, their modification by environment,

their enhancement or diminution by natural selection, what they may. Our special study of the reproductive process has thus fairly brought us to the threshold of a larger inquiry, the primary one of the organic sciences, that of the factors of organic evolution. For it is in nature, as Schiller saw long ago in the human life, which this foreshadows: "While philosophers are disputing about the government of the world, Hunger and Love are performing the task."

SUMMARY.

1. A brief review of the history of evolution theories, and of the present state of the question.

2. A reproductive factor in evolution has been hinted at by a few naturalists.

3. Further indications of the importance in evolution of reproductive and species-regarding, as opposed to the nutritive and self-maintaining activities.

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